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IDENTIFICATION DE CORRIDORS DE DÉPLACEMENTS FAUNIQUES : LIER LES COLLISIONS ROUTIÈRES À LA CONNECTIVITÉ FONCTIONNELLE

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RÉSUMÉ

Actuellement, la stratégie d'atténuation des collisions routières impliquant la faune au Québec est plutôt réactive puisque les mesures de prévention sont adoptées après qu'une zone où une problématique de collisions fréquentes soit identifiée. Il importe donc de développer des approches proactives d'identification des zones à fort risque de collision. La première étape pour atteindre cet objectif est de mieux comprendre où, quand et pourquoi les collisions avec la faune se produisent. Nous avons donc débuté cette étude en analysant 198 collisions impliquant l'orignal (*Alces americanus*) et 252 impliquant le cerf de Virginie (*Odocoileus virginianus*) survenues entre 1990 et 2015 sur l'axe routier 85/185, situé au Bas-St-Laurent (sud-est du Québec, Canada). Nous avons comparé les caractéristiques spatiotemporelles des collisions à un nombre égal de sites distribués aléatoirement le long du tronçon routier. Notre première hypothèse était que les risques de collision sont plus élevés durant les périodes de faible visibilité (nuit) ainsi qu'au cours des périodes de fort débit routier (mois d'été et jours de fin de semaine). Notre deuxième hypothèse stipulait que la distribution spatiale des collisions impliquant les cervidés est modulée par les caractéristiques d'habitat favorables aux cervidés, à leur déplacement et à la capacité des conducteurs de détecter un animal sur la chaussée. Ceci nous a permis de mettre en lumière l'influence des variables topographiques sur le risque de collision avec un orignal et de souligner le caractère davantage imprévisible des collisions avec un cerf dans notre secteur d'étude. Nous avons également noté une augmentation du risque de collision à l'aube et au crépuscule ainsi que durant les mois d'été pour l'orignal, ainsi qu'en mai et à l'automne pour le cerf. Le deuxième volet de ce projet visait à évaluer le pouvoir de validation de différentes métriques de présence faunique, et ce afin de montrer l'importance de la validation des modèles théoriques dans les analyses de connectivité fonctionnelle. Nous avons donc modélisé la connectivité fonctionnelle pour l'orignal et le cerf de Virginie et avons validé ces modèles avec des données empiriques indépendantes. Le processus de validation, qui est souvent négligé dans les études de connectivité, est apparu très sensible aux types de données utilisés, à l'échelle spatiale employée et à l'espèce étudiée. À l'échelle de la route 85/185, nos analyses ont permis de situer les principaux corridors de connectivité avec succès. Le présent mémoire de maîtrise contribue par conséquent à la réflexion, à la proposition d'outils et à l'élaboration de stratégies d'atténuation potentiellement efficaces et robustes des collisions routières avec la faune à l'échelle de notre aire d'étude, tout en offrant un potentiel d'inférence et d'exportation intéressant pour des problématiques similaires ailleurs et avec d'autres espèces.

Mots clés : cervidés, collision routière, connectivité fonctionnelle, échelle spatiale, écologie routière, modélisation, stratégie d'atténuation, validation

ABSTRACT

The mitigation strategy to address wildlife-vehicle collisions in Québec is currently rather reactive, as prevention measures are often adopted after an area of high collision rate has been identified. It is therefore important to develop proactive approaches to identify these areas of high collision risk. The first step in achieving this objective is to better understand where, when and why wildlife-vehicle collisions happen. We therefore began this study by analyzing 198 collisions involving moose (*Alces americanus*) and 252 collisions involving white-tailed deer (*Odocoileus virginianus*) that happened from 1990 to 2015 on the 85/185 road axis in the Bas-St-Laurent region (southeastern Québec, Canada). We compared spatiotemporal characteristics at collision sites with an equal number of sites distributed randomly along the road axis. Our first hypothesis was that collision risk would be greater in periods of low visibility (at night) and during periods of higher traffic volume (summer months and weekends). Our second hypothesis was that the spatial distribution of cervid-vehicle collisions would be modulated by habitat factors that are suitable for cervids, their movement and a motorist's capacity to detect an animal on the road. This allowed us to highlight the influence of topographic variables on collisions involving moose and the more unpredictable nature of collisions involving deer in our study area. We also noted an increase in collision risk at dawn and dusk as well as during summer months for moose and in May and fall for deer. The second part of this project aimed to evaluate the validation strength of different wildlife presence metrics in order to show the importance of validating theoretical models in functional connectivity analyses. We therefore modeled functional connectivity for moose and white-tailed deer and validated these models with empirical and independent data. The validation process, which is often overlooked in connectivity analyses, appeared very sensitive to the types of data used and spatial scale used and to the species studied. At the scale of the 85/185 road axis, our analyses allowed to successfully locate the main connectivity corridors. This thesis therefore contributes to the reflection related to the mitigation strategies, the proposal of tools and the development of potentially efficient and robust mitigation strategies for road collisions with wildlife throughout our study area, offering interesting inference and export potential for similar issues elsewhere and with other species.

Keywords: cervids, functional connectivity, mitigation strategies, modeling, road collisions, road ecology, spatial scale, validation

TABLE DES MATIÈRES

LISTE DES FIGURES

INTRODUCTION GÉNÉRALE

La population humaine connaît une croissance importante depuis les dernières décennies (Steffen *et al.* 2011; Pereira *et al.* 2010) et cette forte croissance a engendré un besoin grandissant en ressources (Rands *et al.* 2010). Pour ce faire, la population humaine a grandement modifié le paysage mondial afin d'avoir un meilleur accès aux ressources mais aussi pour augmenter la production de ces ressources (Barnosky *et al.* 2012; Motesharrei *et al.* 2014). À ce titre, la population humaine a transformé entre 33 et 50% des habitats terrestres naturels à des fins d'exploitation des ressources (Vitousek *et al.* 1997), ce qui représente une modification plus importante que la dernière période glaciaire (~30%; Barnosky *et al.* 2012). Le changement de vocation des terres le plus important est le passage des terres à vocation forestière vers l'agriculture intensive (Pereira *et al.* 2010). Les impacts de ces modifications des paysages naturels suscitent un grand intérêt de la part des écologistes (Ewers *et al.* 2010), que ces changements soient liés à l'agriculture (Shiva 2016), à l'exploitation forestière (Bicknell *et al.* 2015) ou à l'exploitation minière (Bell & Donnelly 2006). Cependant, l'une des plus grandes perturbations est sans contredit l'implantation et le développement du réseau routier nécessaire à l'exploitation, l'exportation et l'accès aux ressources nécessaires pour supporter la croissance de la population humaine (Perz *et al.* 2012).

Écologie routière

Dans les pays industrialisés, le réseau routier connaît une forte expansion depuis les dernières décennies; il permet d'améliorer la connectivité entre les communautés et l'accès aux services (Forman *et al.* 2003; Straub 2008; Perz *et al.* 2012). Aux États-Unis, la densité moyenne de routes a atteint 1,2 km/km^2 dans les dernières décennies (Forman & Alexander 1998; Straub 2008), soulignant à quel point les routes font partie intégrante du paysage moderne. En effet, plus de 70% des forêts mondiales se retrouvent à moins de 1 km d'une

bordure, souvent représentée par une route (Haddad *et al.* 2015). L'aménagement de ce vaste réseau routier n'est pas sans conséquence, d'où la naissance de la discipline de « l'écologie routière » (*lib. Road ecology*; Forman *et al.* 2003). Les écologistes s'intéressant à cette nouvelle science ont mis en évidence différents impacts des routes sur plusieurs facettes de l'écologie (p. ex. la végétation, le régime hydrique, la balance chimique des sols, la faune) (Forman *et al.* 2003; Coffin 2007; van der Ree *et al.* 2015). La présence des routes dans le paysage a beaucoup été étudiée du point de vue de la géomorphologie afin de déterminer l'impact de ces structures linéaires sur l'érosion et le système hydrique (Pereira *et al.* 2015; Liu *et al*. 2016; Raiter *et al.* 2018). On note généralement une augmentation du ruissellement des eaux en lien avec le compactage des routes pavées et non-pavées (Soulis *et al.* 2015). Ceci a pour effet de diminuer le taux d'infiltration dans le sol et, par le fait même, la quantité d'eau rendue disponible aux plantes (Soulis *et al.* 2015). De plus, la surface des routes a pour effet d'augmenter la vitesse d'écoulement de l'eau de surface vers les cours d'eau tout en augmentant l'érosion des sols en bordure de route ainsi que l'apport de sédiments vers ces cours d'eau (Negishi *et al.* 2008; Thomaz & Peretto 2016). Une augmentation de la pollution aérienne a également été montrée dans les habitats adjacents aux routes, principalement en lient avec une plus grande concentration de particules de grandes tailles dans l'air (Tong *et al.* 2015; Yli-Pelkonen *et al.* 2017). Certaines équipes de recherche travaillent d'ailleurs à développer des techniques de génie végétal visant à contrer de tels effets des routes sur le régime hydrique et la qualité de l'air (Liu *et al.* 2016; Tong *et al.* 2016).

Dans les pays faisant face à d'importantes chutes de neige, l'utilisation de sels de déglaçage sur les routes est une pratique courante (Allert *et al.* 2012; French & van der Zee 2014). Cependant, l'épandage d'une aussi grande quantité de sels peut avoir des impacts sur les écosystèmes comme la mort de plantes en bordure de routes, résultant d'une trop forte concentration en sels ou d'une modification de la chimie des sols (Devitt *et al.* 2014; Schuler & Relyea 2018). Certains travaux ont également montré que l'emploi de sels de déglaçage pouvait avoir un impact sur la mobilisation des métaux lourds (principalement le cadmium et le zinc) se retrouvant sur ou autour des routes (Backstrom *et al.* 2004; Schuler & Relyea 2018). Ces métaux sont donc lessivés vers les cours d'eau où leur concentration augmente,

ce qui engendre une modification de la diversité des invertébrés benthiques (Clements *et al.* 2000; Carlisle & Clements 2005).

Impacts des routes sur la faune terrestre

Les impacts causés par la construction d'une route affectant la faune peuvent être classés en trois catégories : entrave au déplacement, augmentation de la mortalité par collisions routières et modification de la quantité et de la qualité de l'habitat (Forman *et al.* 2003; Fahrig 2003; Jaeger & Farhig 2004). La perte d'habitat associée à la construction d'une route s'opère via une modification du milieu d'origine en une surface pavée (carrossable) ou par le retrait de sa vocation de production naturelle première. La modification de la qualité de l'habitat peut être positive (augmentation de la nourriture disponible, d'habitats de reproduction ou du succès de chasse; Forman *et al.* 2003), ou encore négative (augmentation du dérangement sonore et augmentation du risque de mortalité par collision routière : Trombulak et Frissell 2000; ou par la chasse sportive : Robinson et Bodmer 1999). Les modifications négatives de l'habitat le long du corridor routier peuvent engendrer un comportement d'évitement de la part de certaines espèces, créant ainsi une perte fonctionnelle (aussi nommée perte indirecte) d'habitats (Polfus *et al.* 2011). Tous ces impacts peuvent jouer un rôle important pour la sélection d'habitat des espèces fauniques et engendrer une modification des habitudes de déplacements des animaux (Fahrig & Rytwinski 2009; van der Ree *et al.* 2011). Ainsi, globalement, les routes représentent deux menaces importantes pour la faune, soit la mortalité routière par collision et la fragmentation d'habitats induite par une perte directe d'habitat sous l'emprise de la route et une perte indirecte à proximité de la route.

Mortalité par collision routière

L'augmentation de la mortalité par collision routière représente souvent l'impact négatif le plus évident lié à une forte densité de routes sur les populations animales et à une fragmentation élevée des habitats fauniques (Kramer-Schadt *et al.* 2004; Laurian *et al.* 2012). En effet, en augmentant la fragmentation des habitats, les ressources peuvent se retrouver spatialement agrégées dans un même endroit ou distribuées de manière hétérogène dans le

paysage, parfois de part et d'autre des barrières aux déplacements (Fahrig 2003). Une telle distribution a pour effet d'inciter les individus à se déplacer de parcelle en parcelle afin d'acquérir ces ressources, augmentant ainsi les risques de mortalités si un habitat défavorable (p. ex. une route) se situe entre ces deux parcelles (Kramer-Schadt *et al.* 2004).

Lorsque la fragmentation est induite par un corridor routier, les risques de mortalité sont plus élevés puisque le risque de collision avec un véhicule y est parfois important (Forman & Alexander 1998; Rytwinski & Fahrig 2015). De plus, certaines espèces animales démontrent une attraction envers les routes, et les utilisent davantage qu'attendu selon une distribution aléatoire (Fahrig & Rytwinski 2009; Laurian *et al.* 2012). À titre d'exemple, il a été démontré que certains herbivores fréquentent les bords de routes afin d'avoir accès à une végétation disponible plus tôt au printemps et fréquemment entretenue (donc rajeunie) et conséquemment riche en énergie et en protéines (Grosman *et al.* 2009; Rea *et al.* 2014). Dans les pays devant faire face à des conditions climatiques favorisant l'englacement des routes en hiver, des sels de déglaçage sont utilisés en grande quantité, créant ainsi des mares salines en bordure des routes (Dussault *et al.* 2006; Leblond *et al.* 2006). Or, certains cervidés ont besoin d'une grande quantité de ces minéraux pour leur croissance (Jones & Weeks 1985; Ceacero *et al.* 2014). Étant donné la faible disponibilité de ces minéraux en nature, ces zones ont un fort potentiel attractif pour des cervidés comme l'orignal (*Alces americanus*; Dussault *et al.* 2006) et le cerf de Virginie (*Odocoileus virginianus*; Weeks & Kirkpatrick 1976). Ces ressources jouent un rôle important dans la régulation osmotique, la reproduction, la lactation et plusieurs autres processus physiologiques (Belovsky & Jordan 1981). Elles s'avèrent donc être des éléments nécessaires pour plusieurs espèces de cervidés, concentrant de grandes densités d'individus aux abords des routes (Dussault *et al.* 2006; Leblond *et al.* 2007). Par conséquent, plusieurs individus ont le potentiel d'entrer en collision avec des véhicules puisqu'ils sont davantage présents sur ou près des routes. Ceux qui meurent par collision génèrent de plus une source de nourriture additionnelle, ponctuelle mais prévisible pour d'autres espèces de carnivores et de charognards qui eux risquent également d'entrer en collision avec des véhicules (Antworth *et al.* 2005). Il en résulte donc une augmentation du taux de mortalité animale à proximité des routes (Forman & Alexander 1998; van der Ree *et*

al. 2010), un problème susceptible de compromettre la conservation d'espèces ou de populations à statut précaire, tel que démontré chez la panthère de Floride (*Puma concolor coryi*; McClintock *et al.* 2015) et le cerf des Keys (*Odocoileus virginianus clavium*; Lopez *et al.* 2003).

En plus des risques pour les populations animales, les collisions routières impliquant la faune représentent un danger pour la sécurité routière. Près de 45 000 collisions routières impliquant la grande faune sont rapportées annuellement au Canada causant des dégâts matériels s'élevant à 200 000 000 CAN$ (Tardif & Associates Inc. 2003). Le coût relatif aux collisions impliquant les cervidés varie entre 3 636 et 46 155$ USD/km/année aux États-Unis (Huijser *et al.* 2009). Pour les collisions impliquant les cerfs et les orignaux, respectivement 56% et 78,6% des coûts sont associés à des blessures majeures et/ou des décès. En moyenne, chaque collision impliquant un cerf est évaluée à 6 617$ USD alors que le coût relatif à une collision impliquant un orignal s'élève à 30 760$ USD (en dollars américains de 2007; Huijser *et al.* 2009). Toutefois, il semblerait que ce type d'accident soit distribué de façon non-aléatoire le long des corridors routiers (Clevenger *et al.* 2003; Steiner *et al.* 2014). C'est pour ces raisons que plusieurs chercheurs mettent en place des mesures d'atténuation visant à réduire les risques de collisions tout en assurant la connectivité des habitats, telles que les passages fauniques et les clôtures à faune, à des endroits stratégiques (Clevenger *et al.* 2001; Jaeger & Fahrig 2004; Lesbarrères & Fahrig 2012).

Fragmentation d'habitat

Depuis l'avènement de l'écologie routière, plusieurs chercheurs ont étudié les impacts des routes sur les milieux naturels, la flore et la faune. L'impact le plus reconnu au sein de la communauté scientifique est probablement la fragmentation et la perte d'habitats associées à la construction d'une nouvelle route (Fahrig & Rytwinski 2009; Cai *et al.* 2013; Cosentino *et al.* 2014). Cependant, la perte d'habitat est étroitement liée à la fragmentation des paysages; puisque celle-ci ne peut avoir lieu que lorsqu'il y a perte d'habitat, leurs impacts respectifs sont donc très difficilement dissociables (Fahrig 2003; St-Laurent *et al.* 2009; Hadley et Betts 2016). Plusieurs chercheurs s'entendent pour dire que la fragmentation suite

à une perte d'habitat peut causer une augmentation du nombre de parcelles, une réduction de la taille des parcelles et une augmentation de l'isolement des parcelles (Fahrig 2003; Haddad *et al.* 2015). En plus de la perte d'habitat engendrée par la construction même de la route, les milieux environnants sont fortement altérés par l'augmentation des bordures (ou écotones) autour du corridor routier (Forman & Alexander 1998; Marcantonio *et al.* 2013). Cette augmentation de la représentation des bordures entraîne souvent une modification de la composition végétale aux abords des routes et, par le fait même, une modification de la composition des assemblages d'espèces fauniques fréquentant ces habitats (Trombulak & Frissel 2000). En effet, certains chercheurs ont observé une augmentation d'abondance d'espèces généralistes et une diminution d'abondance d'espèces de forêt d'intérieur à proximité des routes, rendant les espèces spécialistes et de forêt d'intérieur très vulnérable à la fragmentation par les routes (Forman *et al.* 2003; Matthews *et al.* 2014). L'augmentation drastique du taux de fragmentation du paysage peut être liée à un problème de recolonisation des parcelles ayant subi une extinction locale (Husemann *et al.* 2015). Les routes agissent donc comme barrières, empêchant les individus d'une population-source d'accéder aux populations-puits, illustrant un problème de connectivité (Haddad *et al.* 2015).

Importance de la connectivité

Selon Taylor *et al.* (1993), la connectivité se définie comme étant le degré par lequel le paysage permet ou entrave le mouvement d'individus entre les différentes parcelles de ressources. Selon eux, la connectivité joue un rôle clé dans l'acquisition de ressources et interfère avec le potentiel de colonisation dans un contexte de métapopulation. Or, la présence de corridors routiers peut nuire à cette connectivité, non seulement en augmentant la fragmentation d'habitats mais aussi en créant une zone tampon évitée (c.-à-d. perte indirecte d'habitat, *sensu* Polfus *et al.* 2011) par certaines espèces (Alexander *et al.* 2005; Clevenger & Wierzchowski 2006; van der Ree *et al.* 2010). Certaines études ont mis en évidence le comportement d'évitement des routes de plusieurs espèces de mammifères comme le caribou forestier (*Rangifer tarandus caribou*; Leblond *et al.* 2011) l'ours noir (*Ursus americanus*; Waller *et al.* 2011) et le cougar (*Puma concolor*; Dickson *et al.* 2005)

accentuant ainsi la fragmentation du paysage (Coffin 2007; Rytwinski & Fahrig 2015). Il est donc nécessaire d'évaluer cette connectivité afin de mieux comprendre l'effet des routes sur cette dernière.

Les analyses de connectivité peuvent entre autres servir à supporter des stratégies d'aménagement du territoire ou encore de gestion et conservation d'espèces à statut précaire. Par exemple, Pitman *et al.* (2017) ont utilisé des questionnaires distribués au grand public, des photos de caméras automatisées et des données télémétriques afin de bâtir des modèles de probabilité relative d'occurrence pour le léopard (*Panthera pardus*) en Afrique du Sud et ce, à plusieurs échelles spatiales. Ils ont ensuite jumelé les cartes de probabilité d'occurrence qui en résultaient avec des modèles de connectivité basés sur des circuits électriques (« *Circuit-based models* ») pour ainsi modéliser les liens potentiels entre les populations. Ce genre d'approche a aussi été utilisé pour la conservation du guépard asiatique (*Acynonix jubatus venaticus*), mais avec l'emploi de modèles de chemins de moindres coûts (« *least-cost paths* ») (Moqanaki & Cushman 2017). Jarchow *et al.* (2016) ont quant à eux utilisé la théorie des circuits électriques afin de modéliser les corridors de dispersion potentiels dans le cadre de scénarios de réintroduction d'amphibiens.

D'autre part, les analyses de connectivité peuvent servir à orienter le développement du réseau routier, plus particulièrement lors de la sélection des emplacements potentiels voués à l'aménagement de structures d'atténuation des collisions avec la faune (p. ex. clôtures et passages fauniques). Ce genre d'approche a été utilisé dans l'état de Washington alors que la connectivité a été modélisée à l'aide de chemins de moindres coûts de part et d'autre d'une autoroute (Singleton *et al.* 1999). De plus, une équipe de chercheurs ont modélisé la connectivité autour d'une route en créant des espèces virtuelles et en identifiant les endroits les plus appropriés pour la construction de structures de passages fauniques (Mimet *et al.* 2016).

Stratégies d'atténuation des collisions routières

Jusqu'à présent, les stratégies d'atténuation des collisions routières impliquant la faune sont souvent réactives plutôt que proactives (Huijser *et al.* 2016), puisqu'elles sont régulièrement basées sur des données colligées suite à des collisions routières avec la faune. Ce type d'approche, quoique partiellement efficace, ne permet toutefois pas d'identifier les endroits à risque lors de projets de développement d'un nouveau chantier routier. Il subsiste donc un besoin croissant de recherche en écologie routière afin de développer une méthode proactive permettant de cibler de tels corridors prioritaires d'intervention où il serait nécessaire d'investir des ressources afin de réduire les collisions routières impliquant la faune et ce, tout en conservant une bonne connectivité fonctionnelle de part et d'autre de la route. De plus, les coûts engendrés par la construction de structures de passages fauniques sont moins importants lorsque ces structures sont intégrées dès le début du projet de développement routier (Huijser *et al.* 2009).

Les cervidés comme modèle d'étude

L'orignal et le cerf de Virginie sont responsables de la majeure partie des accidents routiers impliquant la faune au Québec; en effet, il survient en moyenne 650 collisions liéesà l'orignal (MFFP, *données non publiées*) et 6 450 collisions liées au cerf de Virginie à chaque année sur les routes du Québec (MTQ, *données non publiées*). Au Bas-Saint-Laurent, ces deux espèces de cervidés ont été à l'origine de 450 collisions sur l'axe routier 85/185 entre 1990 et 2015 (soit 85,6% des collisions impliquant la faune sur cette route). De ces collisions, 50 ont engendré des blessures aux automobilistes, 217 ont engendré des dégâts matériels majeurs et une a malheureusement causé le décès d'au moins un automobiliste (MTMDET, *données non publiées*). Ce nombre élevé de collisions routières impliquant les cervidés fait de ces espèces des modèles biologiques de choix lors d'études en écologie routière. Cette réalité est d'autant préoccupante que ces deux cervidés sont reconnus pour démontrer une attraction pour les bords de routes, que ce soit induit par la végétation fréquemment entretenue (et donc hautement nutritive, digestible et accessible; Rea & Gillingham 2001; Myneni *et al.* 2007) ou à la présence de mares salines (Leblond *et al.* 2007; Grosman *et al.* 2009).

Toutefois, les cervidés représentent également un moteur socioéconomique important, relativement aux coûts liés aux accidents et aux opportunités d'exploitation cynégétique. En effet, les collisions avec les cervidés induisent des coûts (bris matériel, capital humain) importants, ayant été estimés à 97 000 $/accident avec l'orignal et 15 000$/accident avec le cerf (en dollars canadiens de 2013) en 2016 (MTMDET 2016). Les collisions impliquant l'orignal sont souvent les plus sévères considérant la stature de ce cervidé qui risque de basculer dans le pare-brise puis dans l'habitacle du véhicule impliqué dans la collision (Dussault *et al.* 2006; MTMDET 2016; Niemi *et al.* 2017). De plus, les mesures d'atténuation visant à diminuer les collisions routières avec ces deux cervidés peuvent avoir des retombées importantes, tant sur le plan écologique que socioéconomique, à la lumière de l'importance de ces deux espèces tant pour la province de Québec que pour la région du Bas-Saint-Laurent. En effet, en 2010, 169 567 permis de chasse à l'orignal ont été vendus aux chasseurs résidents du Québec pour un revenu total de 9 507 621$ (MRNF 2012). De plus, les chasseurs d'orignaux du Québec ont dépensé 204 000 000$ en 2012 afin de s'adonner à leur activité (Écoressources 2014). Selon cette même source, les 38 500 chasseurs bas-laurentiens ont cumulé 379 000 jours-chasse et ont dépensé 35 800 000$ en 2012 dans le but de chasser, la chasse à l'orignal représentait la majeure partie de ces activités. En plus des revenus directs et indirects nommés précédemment, la chasse à l'orignal a généré 1 885 emplois à temps complet pour l'ensemble de la province en 2012 (Écoressources 2014). Au Bas-Saint-Laurent, 4 124 orignaux ont été récoltés lors de la saison de chasse 2017 plaçant la région au 3^{e} rang pour le nombre d'animaux récoltés après la Gaspésie et le Lac-Saint-Jean (MFFP 2017). Pour le cerf de Virginie, environ 140 000 chasseurs ont généré 78,2 millions de dollars dans le but d'exercer leur activité de chasse en 2000 (Huot et Lebel 2012). Au Bas-Saint-Laurent, 7 357 permis de chasse au cerf de Virginie ont été vendus en 2007, générant près de 368 000$ (Écoressources 2014). La chasse en général crée 1 045 emplois à temps complet et engendre 94,63$/habitants en PIB au Bas-Saint-Laurent (Écoressources 2014).

À la lumière de l'importance socioéconomique de ces deux espèces de cervidés mais également en regard des risques qu'ils constituent pour la sécurité publique, mettre en place des mesures d'atténuation (p. ex. passages sous la route, barrières anti-cervidés, passages surélevés) visant à réduire les collisions entre la faune et des véhicules et ainsi diminuer les blessures et mortalités chez les usagers de la route, représente un enjeu incontournable auquel s'est intéressé le présent mémoire de maîtrise.

Objectifs et résultats

L'objectif principal de cette étude était de développer une méthodologie pour la modélisation et la validation de corridors fauniques dans le cadre de projets routiers. Plus précisément, notre premier objectif était de caractériser les patrons temporels et spatiaux impliquant les cervidés (Chapitre 1). Notre deuxième objectif visait à développer une méthode d'identification et de validation des corridors de déplacements de la faune afin de déterminer les zones prioritaires pour l'aménagement de structures d'atténuation et d'évaluer le pouvoir de validation de différentes métriques de présence faunique (Chapitre 2).

Pour notre premier objectif, nous avons émis l'hypothèse que le risque de collision serait influencé par les patrons d'activité humaine et de déplacements fauniques. Nous prédisions donc que le risque de collision serait plus élevé là où la sinuosité de la route serait élevée et durant la nuit, l'aube et le crépuscule (influençant la visibilité et le temps de réaction des automobilistes), mais aussi durant les jours de fin de semaine et les mois d'été (mai à août), des périodes durant lesquelles le débit routier devrait être plus élevé. Notre deuxième hypothèse était que le risque de collision serait modulé par les caractéristiques d'habitat favorables aux cervidés, leur taux de mouvement ainsi que la capacité des automobilistes à détecter un animal sur la chaussée. Nous avons donc prédit que les collisions avec l'orignal et le cerf se produiront plus souvent à proximité des mares salines, des fonds de vallée et des zones d'habitat favorable (utilisé ici comme proxy de densités de cervidés plus élevées).

Nos travaux ont montré que les collisions impliquant les cervidés sur l'axe 85/185 ne sont pas distribuées de façon homogène ni dans le temps, ni dans l'espace (Chapitre 1). Pour l'orignal, il était possible d'observer une augmentation des collisions à l'approche du printemps avec un maximum au milieu de l'été. La distribution des collisions impliquant le cerf était légèrement différente puisqu'on observait un premier maximum de collisions en avril ainsi qu'une deuxième augmentation à l'automne qui culminait en septembre. De plus, un nombre plus important de collisions se produisaient durant les périodes de faible visibilité (nuit, aube et crépuscule) pour les deux cervidés. Les caractéristiques topographiques semblaient avoir un fort effet sur le risque de collision avec un orignal. Nos résultats nous ont aussi permis de mettre en évidence l'importance de valider les modèles de connectivité théoriques (Chapitre 2). Ce type de modélisation nous a également permis d'identifier les sites où la probabilité qu'un orignal ou cerf traverse la route était plus élevée, permettant ainsi d'identifier les secteurs à risque pour les collisions routières. Nous avons également souligné l'effet du type de données utilisées pour valider les modèles ainsi que l'espèce cible sur la puissance de validation des modèles.

CHAPITRE 1
AU MAUVAIS ENDROIT AU MAUVAIS MOMENT : LES PATRONS DE DÉPLACEMENTS DES ORIGNAUX ET DES CERFS DE VIRGINIE INFLUENCENT LE RISQUE DE COLLISION ROUTIÈRE

Cet article sera soumis dans la revue internationale révisée par les pairs *Accident Analysis and Prevention* à l'été 2018. Une version français a également été publiée dans un numéro spécial du Naturaliste Canadien[1].

1.1 RÉSUMÉ EN FRANÇAIS DU PREMIER ARTICLE

Les stratégies d'atténuation des collisions routières impliquant la faune requièrent des connaissances suffisantes sur les causes, les lieux et les circonstances de ces collisions afin de représenter des outils efficaces permettant d'améliorer la sécurité routière. Les collisions avec les cervidés sont connues pour être influencées par certains facteurs spatiaux tels que la topographie et le couvert forestier. Cependant, les changements temporels dans le comportement des animaux et des automobilistes sont souvent négligés, bien qu'ils puissent augmenter les risques de collision entre les cervidés et les véhicules. Conséquemment, nous avons évalué les facteurs influençant la distribution spatiotemporelle de 450 collisions avec l'orignal et le cerf de Virginie sur un tronçon de 100 km d'autoroute dans le sud est du Québec, Canada. Les facteurs spatiaux et temporels expliquaient efficacement la distribution des collisions impliquant l'orignal, mais pas les collisions impliquant le cerf de Virginie, suggérant que ces dernières se produisaient plus aléatoirement le long de l'autoroute. Le risque de collision impliquant l'orignal était principalement modulé par les variables topographiques et d'habitat, car les interactions entre la pente et l'altitude et entre la pente et la distance à une parcelle de bon habitat pour l'orignal avaient un fort effet sur le risque de collision. La sinuosité de la route et la proportion de peuplements résineux matures autour des points de collision influençaient positivement le risque de collision impliquant les cerfs. Une augmentation temporelle du nombre de collision a été notée à différentes périodes biologiques durant lesquelles les taux de mouvements sont connus pour être plus élevés (c.-à-d. dispersion post-hivernale et rut). Ces résultats suggèrent que les déplacements des cervidés sont le principal facteur

1. Laliberté, J. & M.-H. St-Laurent. 2019. Détermination des facteurs spatiotemporels expliquant le risque de collision routière avec des cervidés sur l'autoroute Claude-Béchard (85) au Témiscouata. Naturaliste Canadien, 143: 40-47.

influençant le risque et la fréquence des collisions impliquant les cervidés. Nos résultats indiquent que les stratégies d'atténuation visant à diminuer la probabilité de collision avec les cervidés doivent être propres à l'espèce et devraient se concentrer plus étroitement sur les mouvements des animaux.
***Mots clés* :** Cerf de Virginie (*Odocoileus virginianus*), risque de collision, Orignal (*Alces americanus*), routes.

1.2 IN THE WRONG PLACE AT THE WRONG TIME: MOOSE AND DEER MOVEMENT PATTERNS INFLUENCE WILDLIFE-VEHICLE COLLISION RISK

ABSTRACT

Mitigation strategies for wildlife-vehicle collisions require sufficient knowledge about why, where and when collisions occur in order to be an efficient tool to improve public safety. Collisions with cervids are known to be influenced by spatial factors such as topography and forest cover. However, temporal changes in animal and motorist behaviors are often overlooked although they can increase the odds of cervid-vehicle collisions. Consequently, we evaluated potential factors influencing the spatiotemporal distribution of 450 collisions with moose and white-tailed deer along the 100-km long highway in southeastern Québec, Canada. Both spatial and temporal factors efficiently explained moose-vehicle collisions but not collisions with white-tailed deer, suggesting that the latter occurred more randomly along the highway. The risk of moose-vehicle collisions was mainly modulated by topographic and habitat variables, as the interactions between slope and elevation and slope and distance to suitable moose habitats had a strong effect on collision risk. Road sinuosity and the proportion of mature coniferous stands around the collision site positively influenced deer-vehicle collisions. A temporal increase in collision numbers was noted in different biological periods during which movement rates are known to be higher (e.g. post-winter dispersal and rut). These results suggest that cervid movement is the main factor influencing collision risk and frequency. Our results indicate that mitigation strategies aimed at decreasing the probability of collision with cervids must be species-specific and should focus more closely on animal movement.
Keywords **:** Moose (*Alces americanus*), roads, white-tailed deer (*Odocoileus virginianus*), wildlife-vehicle collisions

INTRODUCTION

Wildlife-vehicle collisions (hereafter referred to as WVCs) have known a great worldwide increase during the last decades (Seiler *et al.* 2004; Huijser *et al.* 2008; Morelle *et al.* 2013), becoming an important threat to road safety (Bissonnette *et al.* 2008). As the road network keeps expanding annually (Hawbaker *et al.* 2006), this temporal trend is expected to persist (van der Ree *et al.* 2015a). This increase in WVCs can be partially explained by either one or a combination of the following factors: an increase in vehicule traffic (Ng *et al.* 2008; Sudharsan *et al.* 2009), an increase in regional wildlife densities (Gunson *et al.* 2011; Niemi *et al.* 2017) and shifts in resource distribution (Seiler *et al.* 2004; Keken *et al.* 2016). Nearly 45,000 collisions with large wildlife are reported each

year in Canada, a number that seems to increase annually (Huijser *et al.* 2008; 2009). In 2007, the cost of cervid-vehicle collisions varied from 3,636 to 46,155 USD per km per year in the United States (Huijser *et al.* 2009). On average, a collision with a deer (*Odocoileus spp.*) costs $6,617 (in 2007 USD) compared to $30,760 for a collision with a moose (*Alces americanus*) (Huijser *et al.* 2009). For deer- and moose-vehicle collisions, 56% and 79% (respectively) of the costs were associated with major injuries or deaths.

WVCs are rarely randomly distributed (Mkanda & Chansa 2011; Steiner *et al.* 2014; Santos *et al.* 2017), instead being influenced by different factors that can vary in space and time. Many ecologists have studied the temporal and spatial patterns of wildlife-vehicle collisions (e.g. Bashore *et al.* 1985; Finder *et al.* 1999; van der Ree *et al.* 2015b; Rea *et al*. 2018), ultimately pointing out four types of factors that can influence collision risk: 1) regional densities of wildlife species, 2) traffic rate (but see Grilo *et al.* 2015), 3) wildlife resource distribution and availability along roads, and 4) scale-dependent temporal changes in wildlife and driver behaviours.

Fluctuation of both wildlife densities and human activities is recognized as a major factor explaining variations in the number of WVCs. For instance, in Belgium, a constant increase in WVCs was observed over an 8-year period (2003 to 2011), during which 3,965 WVCs were reported and related to an increase in abundance of the main species involved in the collisions (Morelle *et al.* 2013). Similar trends were noted in Finland (Niemi *et al.* 2017) and in Northeastern United States (Litvaitis & Tash 2008), where increases in moose (*Alces alces* in Europe) densities have been shown to influence the number of WVCs. In addition, the number of WVCs has been shown to increase with traffic volume (Seiler *et al.* 2004; Litvaitis & Tash 2008; Niemi *et al.* 2017), although a higher traffic volume was also identified as a deterrent factor for some species to approach and cross roads (Olson *et al.* 2015).

The distribution of resources important for wildlife is another factor known to modulate the occurrence and the number of WVCs via its influence on animal movement. For example, Hurley *et al.* (2008) reported that models including habitats predicted moose-vehicle collisions better than all models including only driver-related variables in Mount

Revelstoke and Glacier National Parks. Other studies have highlighted that WVCs were more likely to occur near patches of suitable habitat and where roads crossed valley bottoms (Dussault *et al.* 2006; Gunson *et al.* 2011). In addition, certain resources can have a particularly attractive effect on animals, increasing the risk of WVC; for example, moose are known to actively seek salt pools found near roads in late spring when the snowmelt drains de-icing material, therefore creating a hotspot of WVC (Dussault *et al.* 2006; Grosman *et al.* 2011; Rea *et al.* 2014).

Temporal changes in animal behaviour could have a strong influence on the probability of WVCs. Several studies have suggested that increasing numbers of WVCs during early summer and fall are often related to punctual increases in movement rate, such as during mating and post-natal dispersal (Dussault *et al.* 2006; Smith-Patten & Patten 2008; Danks & Porter 2010; Morelle *et al.* 2013). A variation in the occurrence of WVCs was also noted between daily phases, with a distribution of collisions skewed towards the night with peaks also observed during dawn and dusk (Kusta *et al*. 2014; Colino-Rabanal *et al.* 2018). Common hypotheses used to explain such observations range from an increase in movement rate for the species involved in WVCs to their lower detectability by motorists (Dussault *et al.* 2006; Morelle *et al.* 2013). In fact, two main factors could affect a motorist's capacity to detect an animal on the road: luminosity (Rodgers & Robins 2006) and road sinuosity (Kim *et al.* 2007; Zuberogoitia *et al.* 2014).

Accidents with large mammals (e.g. cervids) are considered a major threat to road safety (Bissonette *et al.* 2008; Huijser *et al.* 2009), supporting the need to investigate the patterns involved in the distribution of these collisions. Understanding why, where and when collisions with cervids occur is a crucial step in the identification of appropriate locations for mitigation structures (e.g. wildlife underpasses, overpasses and fences) (Dussault *et al.* 2006; Neumann *et al.* 2012) and to develop a proactive method to address this issue. Such analyses help guide mitigation strategies and focus measures on the modification of wildlife behavior or on the education of motorists concerning collision risks. Our objective was thus to characterise the temporal and spatial distribution patterns of road collisions with moose and white-tailed deer (*Odocoileus virginianus*) and to identify factors that could explain these patterns. We hypothesised that collision risk is

influenced by temporal variations in traffic rate and in wildlife movement patterns. We thus predict that collision risk will be greater at night, dawn and dusk (influencing driver's visibility and reaction time, and cervid activity), but also during weekends, when rate volume should be higher, and during summer months (May to August), when cervid movement rates are higher. In addition, we hypothesised that spatial factors influencing habitat suitability to cervids, their movement patterns and the capacity of drivers to detect animals on the road modulate the collision risk. We predict that collisions with moose and deer will occur more often closer to salt pools, valley bottoms, near suitable habitats (as a proxy of higher moose and deer local densities), where road sinuosity is greater and on rainy days.

METHODS

Study area

We conducted our study along the 85/185 highway, located in southeastern Québec, Canada. This region is representative of the balsam fir (*Abies balsamea*) – yellow birch (*Betula alleghaniensis*) domain. Dominant tree species are balsam fir, white spruce (*Picea glauca*), yellow birch, white birch (*B. papyrifera*) and northern white-cedar (*Thuja occidentalis*) (Robitaille & Saucier 1998). The large- and medium-sized mammal species encountered in this region are moose, white-tailed deer, black bear (*Ursus americanus*), coyote (*Canis latrans*), red fox (*Vulpes vulpes*) and Canada lynx (*Lynx canadensis*). Moose densities are amongst the highest in eastern Canada, with densities reaching 0.5 moose/km^2 (MFFP 2016) with regional peaks at 2.3 moose/km^2 (Ross *et al.* 2014). In contrast, deer densities of 9.46 deer/km^2 were found in the wintering grounds when surveyed in 2006 (MRNF, unpublished data). The absence of wolves (*Canis lupus*), extirpated from the south shore of the St. Lawrence River ~150 years ago, and intensive timber harvesting as well as suitable moose management plans have supported these very high cervids densities. Winter harshness is the main factor influencing deer densities in this region (Lesage *et al.* 2001). This region is characterised by a mean elevation of 290 m and low rolling hills (slopes of 7% on average) (Robitaille & Saucier 1998). The mean annual temperature is 2.5°C with precipitations ranging from 900 to 1000 mm of which 35% falls as snow. Forested habitats dominate the landscape (~85%), but agriculture (~15%) and urban spaces (~10%) are also

common. Several small rural and agricultural villages are distributed throughout the entire region (Robitaille & Saucier 1998).

The 85/185 highway is the main road axis connecting the city of Rivière-du-Loup (Québec) to the New Brunswick border. This 100-km road has been undergoing major roadwork since 2001 to be enlarged from a two-lane provincial highway to a four-lane divided highway. The speed limit is currently set at either 90 or 100 km/h depending on the road segment. Traffic varied from 840 to 12,600 cars/day/km with an average value of 7724 cars/day/km (Ministère des Transports, de la Mobilité Durable et de l'Électrification des Transports, hereafter MTMDET 2015).

Collision data

We consulted the WVC archives of the Société de l'Assurance Automobile du Québec (SAAQ) in order to build a database of WVCs recorded on the 85/185 highway between 1990 and 2015. The motorists involved in the accidents reported each individual collision to the SAAQ and some important variables were noted: the speed limit on the road segment, the date of the collision, the animal species and the number of animals involved in the collision, as well as several variables referring to injuries to the driver and passengers and damages to the car. We only kept cervid-caused collisions (moose and white-tailed deer; hereafter deer) for analyses as other species represented a very small proportion of the accidents reported (*e.g.* black bear with 2.07% of the WVCs). We then divided the data in two datasets, one for each cervid species (moose; n=198, deer; n=252).

Geomatic data

We used 1 : 20,000 numerical ecoforest maps published by the Ministère des Forêts, de la Faune et des Parcs (hereafter MFFP) and updated every two years to integrate natural and anthropogenic disturbances. Minimum mapping unit size was 4 ha for forested polygons and 2 ha for non-forested areas (e.g., water bodies). Land-cover polygons were classified into 11 categories (Table 1). We used numerical 1 : 20,000 maps of roads and topography (to estimate elevation and slope) published by the MFFP; this organisation also

provided the location of moose and white-tailed deer wintering grounds (used here as a proxy for cervid densities), delineated by aerial surveys.

We used telemetry data collected on 20 moose in the Témiscouata region and 100 deer in the Témiscouata and Pohénégamook regions to build and map Resource Selection Functions (RSF; Manly *et al.* 2002) for both species (see Suppl. Mat. 1-2) in order to identify the areas of high occurrence probability of cervids. The threshold used to select these areas differed between species (2.5% highest ranked habitats for moose and 10% for white-tailed deer) because of the differences in habitat quality for the two species; indeed, almost the entire study area is composed of high occurrence probability habitats for moose, so we lowered the threshold for this species to pinpoint the most suitable patches and increase contrast with the remaining patches. Annual average daily traffic and the configuration of the future highway were shared by the MTMDET. To create the sinuosity index, we divided the road in 1-km segments and calculated the road sinuosity using the Calculate Sinuosity tool of ArcGIS 10.1 for each 1-km road segment. This tool calculates the sinuosity of a line segment by dividing the shortest possible path by the total length of the segment. This index varies between 0 and 1 (where 1 represents a straight line; ESRI 2011). We identified location of salt pools and streetlights during field visits and used the location of streetlights to create a binary luminosity index (presence or absence of streetlights in a 50-m radius buffer centered on the road axis) along the road. We used the location of pools of backwater, which we considered to be saltpools, to calculate the distance to the nearest salt pool. Finally, we obtained climate and meteorological data from 6 meteorological stations installed near the 85/185 highway by the Ministère du Développement Durable, de l'Environnement et de la Lutte aux Changements Climatiques, and extracted meteorological variables from the station closest to the collision and random locations.

Temporal analysis

We assessed the effect of month, day of the week and daily phases (dawn, day, dusk, night) on the temporal distribution of cervid-vehicle collisions. Daily phases were differentiated using the official time of sunrise and sunset (NRC 2017), where the dawn and dusk periods were identified by adding and subtracting 30 minutes to the time of sunrise and sunset, respectively. Day and night were then identified as the periods in between.

For each species, we first tabulated the number of collisions for each year, month, day of the week and daily phase and then obtained a collision count for each temporal period. We then evaluated the effect of months, day of the week and daily phases using a Poisson regression (PROC GLIMMIX; SAS Software 9.4). The duration of the period was used as an offset variable in order to account for the variation of daylight duration throughout the year. We conducted multiple comparisons of least squared means using the SAS macro MULT (Piepho 2012) with a Bonferroni correction. We performed variance partitioning for the three temporal variables (daily phase, day of the week and month) and their intersections based on the adjusted R-squared (Legendre & Legendre 1998) that we obtained for each model combination using the SAS macro developed by Mittlbock (2002). Variance partitioning was used to calculate the proportion of explained variance by each independent variable and each combination of these variables, allowing us to identify the temporal period that had the strongest effect on the collision distribution. The variance explained by each combination was standardized with the proportion of total variance explained in order to allow comparisons between both cervids independently of model fit.

Spatial analysis

For each species, we assessed the effect of spatial factors on the probability of cervid-vehicle collisions by comparing characteristics from each collision location to those of an equal number of random points distributed along the highway. Characteristics at the collision site were classified in three categories: habitat, meteorological or driver-related variables. Based on the yearly variations in collision rate (Figure 1), we only tested the impacts of spatial factors during the months of higher cervid activity (from April to

September for moose, and from April to October for deer) in order to reduce potential bias associated to the rare collisions occurring during winter. In addition, collisions for which we did not have meteorological data were removed from the database, so sample size was then reduced to 155 moose-vehicle collisions and to 168 deer-vehicle collisions.

The group of habitat variables comprised elevation (m), slope (°), the land-cover category (under the collision or random location), the proportion of wetlands and mature coniferous stands in a buffer and the distance to the nearest salt pool (m), wintering ground (m) and patch of high occurrence probability (hereafter DHOP, m). As in Leblond *et al*. (2011), we tested different buffer sizes using the Bayesian Information Criterion (BIC; 500, 1000, 1500, 2000 and 2500m) to contextualize the variation in elevation and slope around the collision or random location. We kept buffer sizes of 500 m for slope and elevation for both cervids. A decay distance transformation ($e^{-\alpha/d}$; Carpenter *et al.* 2010) was used to attenuate the influence of an increasing distance to features rarely encountered (such as the nearest salt pool, the nearest wintering ground and the DHOP). To do so, we tested the effect of different alpha values (50, 150, 250, 500, 750, 1000, 2000, 3000, 4000) as in Lesmerises *et al.* (2018) and compared them using the BIC. All variables were kept untransformed except for the DHOP for moose, for which a decay distance transformation with an alpha value of 150 ($e^{-150/d}$) was kept; the effect of this variable plateaued at a distance of 1 km.

Meteorological data comprised maximum and minimum daily temperature (°C) and daily precipitation (mm). Daily precipitation was converted into a binary variable (rain or not). We only used rain instead of rain and snow or total precipitation because the majority (98.5% for moose and 90% for deer) of collisions occurred during the snow-free period. In order to compare climatic variables between collision locations and random points, we needed a date to assign climatic variables to random points. To do so, a date was randomly chosen within a ± 1-week time window centered on the real collision date; the meteorological variables corresponding to that date were then attributed to the random point, which was paired to the collision location.

Finally, driver-related variables included the sinuosity index of the 1-km road segment, the luminosity binary index and the traffic rate. We used the Variance Inflation Factor (VIF) and the condition index in order to verify the absence of multicolinearity among variables; the VIF was respectively < 1.64 and < 1.01 for moose and deer, while the condition index was < 11.09 and < 15.65 for the two species. Minimum temperature was removed from further analyses due to high collinearity with the maximum temperature. We built candidate models (see Table 2 for moose, and Table 3 for deer) based on different hypotheses: road variables, meteorological conditions, land-cover category, topography and points of interest (salt pools and wintering grounds). We ran conditional logistic regressions using the Survival package (Therneau 2015) in R (R Core Team 2017). We used the BIC to select the most parsimonious model because the number of parameters in our models varied greatly, and the BIC is recognized to be more punitive than the AIC (Burnham and Anderson 2003). We validated our most parsimonious models using *k*-fold cross-validations (Boyce *et al.* 2002) adapted for conditional logistic regression (see Leblond *et al.* 2010) using 80% of the database to assess its robustness. We evaluated the robustness of our models by calculating the percentage of collisions that the model classified as real events based on 20% of the database.

RESULTS

The average number of collisions per year reached 7.62 (± 3.20 SD) for moose and 9.58 (± 3.46 SD) for deer along the 100-km highway. For both species, the number of collisions varied only between months (moose: $F_{(10, 288)} = 125.84$, $P < 0.001$; deer: $F_{(11, 315)} = 16.83$, $P < 0.001$) and daily phases (moose: $F_{(3, 288)} = 385.22$, $P < 0.001$; deer: $F_{(13, 315)} = 646.40$, $P < 0.001$), as the day of the week had no effect on the number of collisions (moose: $F_{(6, 288)} = 0.88$, $P = 0.512$; deer: $F_{(6, 315)} = 1.06$, $P = 0.3838$). Differences in least squared means highlighted an increase in moose collisions in late spring with a maximum in early summer (June; Figure 1a) and a first maximum of deer collisions in April followed by a second increase in fall, centered in September (Figure 1b). The analysis of the least squared means for daily phases revealed a higher number of collisions during dawn, dusk and night compared to daytime for moose (Figure 2a) and during dawn and dusk compared to the day and night for deer (Figure 2b).

Variance partitioning showed that the main factors explaining variation in the moose collision distribution were the daily phases (92.80%) and months (83.72%), while for deer only months (with 102.58% of the explained variance) had an important effect (Figure 3). Percentages higher than 100% were possible because some periods had negative effects. Double intersections displayed negative values (e.g. shared variation between daily phases and months for moose), indicating that these two independent variables explained more variation together than the sum of their individual effects (Legendre & Legendre 1998). These negative portion of variance should, however, be interpreted as null values (Legendre & Legendre 1998).

Spatial analysis

The most parsimonious model explaining the variability in spatial distribution of moose-vehicle collisions included elevation, slope, DHOP and interactions between those variables (Tables 2 and 4). Collision risk was generally greater at higher elevations but decreased as slope increased (Figure 4a). Also, collision risk was high near patches of high moose occurrence probability but decreased with distance in areas with steep slopes (Figure 4b). This model was robust and successfully separated random points from collisions in 71.6% of the cases (± 7.0 SD).

The most parsimonious model explaining spatial variations in collisions with white-tailed deer only included road sinuosity and proportion of mature coniferous stands in a 500-m buffer zone (Tables 3 and 5). A second model differed by only 2.79 in ΔBIC from the most parsimonious one. This second model included the proportions of mature coniferous stands and of heavily disturbed habitats. The most parsimonious model suggests that collision risk was greater where road sinuosity and proportion of mature coniferous stands were higher. However, this model was not robust and separated random points from collisions in only 60.3% of the cases (± 7.4 SD).

DISCUSSION

Our results demonstrate that both spatial and temporal factors explained the distribution of cervid-vehicle collisions on the 85/185 highway. Our first hypothesis, stipulating that cervid-vehicle collisions would be modulated by temporal factors, was supported for moose as 78.13% of the temporal variance was explained, while variables included in the most parsimonious model were less efficient at explaining temporal variance in deer-vehicle collisions (42.04%). This same pattern was observed for our second hypothesis concerning the influence of spatial factors on cervid-vehicle collisions. This suggests that deer-related collisions may be less predictable than moose-related collisions.

Cervid movements

Based on our results, we found that spatiotemporal patterns of cervid movement were the main factor influencing the probability of road collisions. Increases in collisions with cervids coincided with periods during which moose and deer tend to use habitats that are closer to roads or during periods with greater movement rates, namely spring (April to June), fall (September to November) and at dusk, night and dawn. In addition, some spatial factors were identified as important drivers of increase in collision probabilities.

Plant growth occurs earlier on roadsides than in forest in spring (late April; Rea & Gillingham 2001), which could be attractive for an herbivore. This is mainly attributed to increased sunlight (Wright & van Schaik 1994; Myneni *et al.* 2007), increased heat-sum (Deslauriers *et al.* 2008; Seo *et al.* 2008) and frequent vegetation management which increases the herbaceous cover (Rea & Gillingham 2001). Such management practices increases the availability of highly digestible food sources that are rich in proteins and attractive for cervids (Dumont *et al.* 2005). During the harsh winter months, cervids mainly eat deciduous and coniferous twigs with high secondary compounds (tannins and phenolic compounds; Stolter *et al.* 2005) that could lower protein digestibility and palatability (Spalinger *et al.* 2010), triggering a depletion of body reserves associated with a lower energy intake and metabolization (Christiansson & Creel 2009). In addition, late spring and early summer coincide with the calf-rearing period, during which lactation, a highly demanding process for female ungulates (Parker *et al.* 2009), is associated with an increase

in food intake (Parker *et al.* 1990; Richard *et al.* 2017). In order to recover body mass in early spring, cervids seek highly digestible vegetation, especially terminal twigs and herbaceous plant biomass (Dumont *et al.* 2005; Wam & Hjeljord 2010). To optimize ingestion of easily digestible energy and proteins, ungulates synchronize their movements with the vegetation phenology to have access to green vegetation for a longer period (i.e. green-wave hypothesis; Zeng *et al.* 2010; Bischof *et al.* 2012; Riverud *et al.* 2016), which could explain a higher rate of use of roadsides during spring. This hypothesis is mainly used to explain large-scale migrations such as those observed in red deer populations, which are known to follow the phenological gradient of vegetation through their migration (Bischof *et al.* 2012).

Cervids are also known to consume resources with high concentrations of minerals when their physiological requirements inincrease (Ceacero *et al.* 2010; Estevez *et al.* 2010), principally due to antler growth for males (April to May; Cappelli *et al.* 2015) and lactation for females (May to July; Hackman 2011; Richard *et al.* 2017). As some important minerals (e.g. Na) are scarce and insufficient in terrestrial vegetation during these periods (Belovsky 1978; Estevez *et al.* 2010; Ceacero *et al.* 2014), roadside salt pools, which are 30 times more concentrated in sodium than natural lakes and ponds (Leblond *et al.* 2007), become very attractive resources for moose and deer. Our spatial models did not identify salt pools as important factors influencing collision risk, which may be linked to the fact that we did not measure salinity in our salt pools and that some salt pools might have been missed during our field surveys if not visible from the road.

Natal dispersal, characterised by increased movements rates in young deer (Long *et al.* 2005; Putzu *et al.* 2015), occurs in late spring (April), potentially increasing the risk of deer collision with a vehicle. In addition, the distribution of deer-vehicle collisions highlighted an increase in the number of collisions from September to November, which could be attributed to the increase in movement rate observed during the rutting season (Diefenbach & Shea 2011), especially for males that are seeking out females (Stickles *et al.* 2016; Whitman *et al.* 2018).

Collisions with deer were more frequent close to mature coniferous stands, an observation that can be related to the increased rates of movement during spring for deer. Indeed, mature coniferous stands are an important habitat predictor of higher deer

occurrence (Lesage *et al.* 2000), especially in late winter when they are getting ready to leave their wintering areas (Diefenbach & Shea 2011), which are mostly dominated by conifers at our latitude (Telfer 1970; Lesage *et al.* 2000). Other studies also highlighted a positive relationship between deer-vehicle collision risk and habitat suitability or deer densities (Meisingset *et al.* 2014; McCance *et al.* 2015). We hypothesized that the effect of mature coniferous stands is magnified during the spring when deer are leaving their wintering areas to gain access to fresher and more digestible vegetation and when yearling males are dispersing from their natal range.

Cervid-vehicle collisions were also more frequent during dawn, dusk and at night, an observation we explain by the higher movement and activity rates found in cervids during those daily phases (Haikonen & Summala 2001; Ager *et al.* 2003; Wichrowski *et al.* 2005; Hothorn *et al.* 2015; Krauze-Grytz *et al.* 2017). The difference inbetween the number of collisionsthe day and night was relatively greater for deer than for moose and could be related to the difference in activity patterns between the two species. White-tailed deer are known to be more crepuscular (Sullivan *et al.* 2016) than moose, which are more active at night (Klassen & Rea 2008).

The results from our spatial analyses suggest that topography has a strong influence on moose-vehicle collision risk. We noted a greater risk of collision at higher elevation, which could seem contradictory with known patterns of moose space use, usually concentrated in valley bottoms (Gillingham & Parker 2008; Leblond *et al.* 2010). However, in our study area, towns, villages and agricultural fields are mostly distributed along the St. Lawrence River valley, at lower elevation, while forest-dominated landscapes suitable to moose are found at higher elevation. Indeed, moose that were collared and monitored using GPS devices were essentially found at elevations ranging between 306 and 486 m while the elevation in our study area ranged from 0 to 663 m (the moose-vehicle collision recorded at the highest elevation was at 460m).

We also highlighted the synergy between slope and distance to the nearest patch of high occurrence probability and between slope and elevation when explaining the spatial distribution of moose-vehicle collision risk. These interactions refer mainly to moose behavior rather than motorist behavior or reaction time. Proximity to a patch of high quality for moose increased the collision risk regardless of the slope, as moose are expected to be

present at greater densities. Moose are known to use mainly valley bottoms (Gundersen *et al.* 1998; Dussault *et al.* 2007) or to move along topographic lines in order to avoid steep slopes (Leblond *et al*. 2010). Therefore, the collision risk should increase at sites where the road axis crosses valleys compared to roads located on hilltops. We found that collision risk increased away from very good moose habitats where slope is gentler, suggesting that moose leaving poor quality habitats might be following valleys to seek for suitable habitats and could then be found more often on roads. Many other studies showed that collisions were more likely to occur where roads are crossing a suitable habitat or where cervid densities were greater (Nielsen *et al.* 2003; Rolandsen *et al.* 2011; Hothorn *et al.* 2015), but our finding that collision risk could be high even when far away from suitable habitats is rarely noted in wildlife-vehicle collision studies.

Traffic volume

We did not observe an effect of weekday on the number of collisions for both moose and white-tailed deer, even while controlling for the confounding variation associated with months and daily phases. This contrasts with results obtained by Dussault *et al*. (2006) who noted an increase in moose-vehicle collisions on Fridays in central Quebec that was associated with an increase in traffic volume on the last day of the workweek. However, patterns of variation in traffic volume were similar on both highways, with ~ 4,500 cars/km on Fridays (ranging from 3,000 to 4,000 on the other days on the 75 highway; Dussault *et al.* 2006) vs. 6,500 cars/km on Fridays (+44%; varying between 5,200 and 6,100 cars/km on the other days) for the 85 highway (MTMDET, *unpublished data*). The similarity in traffic volume for both highways suggests that the collision risk on the 85/185 highway may have been modulated more by animal movements than by motorist behavior since we did not detect an effect of weekdays on the temporal distribution of collisions. Other studies demonstrated no effect of weekday on WVC distribution (Morelle *et al.* 2013), collisions (Rowden *et al.* 2008) or road crossings (Dodd *et al.* 2005), suggesting an avoidance of high-traffic volumes by animals.

Driver reaction time and capacity to detect an animal

Our analysis suggested that collisions with white-tailed deer occurred more frequently at locations where road sinuosity was lower, which could reduce a motorist's reaction time and capacity to react properly to avoid an animal on the road (Rea *et al.* 2018). Several studies showed that higher mortality rates were associated with lower road sinuosity (e.g. Malo *et al.* 2004; Colino-Rabanal *et al.* 2011; Snow *et al.* 2012). Huijser *et al.* (2007) noted that lower sinuosity could be related to an increase in travelling speed, thus reducing reaction time available to react when an animal is found on the road, while Ranapurwala *et al.* (2016) suggested that motorists might be more cautious on curved roads in comparison to straight roads.

In addition, a lower detectability of cervids by drivers could explain why the collision risk was greater during dawn, dusk and at night, which are all phases of lower luminosity (Rodgers & Robins 2006). Rodgers & Robins (2006) studied moose detectability on a road using moose decoys and volunteer drivers. They showed that mean detection distance of a moose at night was 105m (ranging from 23 to 210m) and concluded that motorists might be driving too fast to avoid an obstacle on the road when driving faster than 70 km/h. Therefore, a shorter reaction time at night might increase collision risk. Rea *et al.* (2018) observed that the reaction time of the drivers who collided with a moose was one third that of drivers that avoided the moose. The daily distribution of cervid-vehicle collisions could then be the combined effect of decreased motorist capacity to detecting an animal on the road and increased activity rates by cervids during dawn and dusk.

CONCLUSION

Our study highlights the importance of assessing both temporal and spatial factors when evaluating collision risk with cervids, especially in boreal forests supporting high densities of cervids. In fact, temporal and spatial distributions proved to be closely related. In addition, in our case, we showed that WVCs might be modulated more by animal movements than by motorist behavior. Based on our temporal analyses and results, it would

be advised to adjust road signs during periods of higher collision risk (e.g. dawn and dusk, from May to September) by adding either temporary road signs or blinking signs to keep motorists aware of the danger during these critical periods. Rea (2012) noted that 70% of road signs indicating cervid-vehicle collision risk were misplaced and that after adding new signs in appropriate locations and a public awareness campaign, moose-vehicle collisions decreased by 50%.

In addition, roadside vegetation and salt pools could be managed by cutting vegetation later in the summer (Rea 2012; Hegland & Hamre 2018) and draining and filling salt pools (Leblond *et al.* 2007), thus decreasing the attractiveness of roadsides in spring. Based on our spatial analyses, we recommend to focus mitigation efforts in valley bottoms and sectors with gentler slopes to prevent moose-vehicle collisions, even far away from suitable moose habitats. This finding would be particularly helpful to orient planning of mitigation structures such as wildlife fencing and underpasses, as these structures could help decrease cervid-caused collisions by 98% (Bissonette & Rosa 2012). However, our limited capacity to explain the spatial distribution of deer-vehicle collisions brings us to use precaution when formulating recommendations (see Kriebel *et al.* 2001) for this species, although we underlined the importance of keeping motorists aware of the greater collision risks on straight road segments (Ranapurwala *et al.* 2016). Nevertheless, our study highlights the fact that cervid movements is the main factor influencing the frequency and the risk of cervid-vehicle collisions and that the effect of certain variables on collision risk can vary depending on their interaction with other relevant variables.

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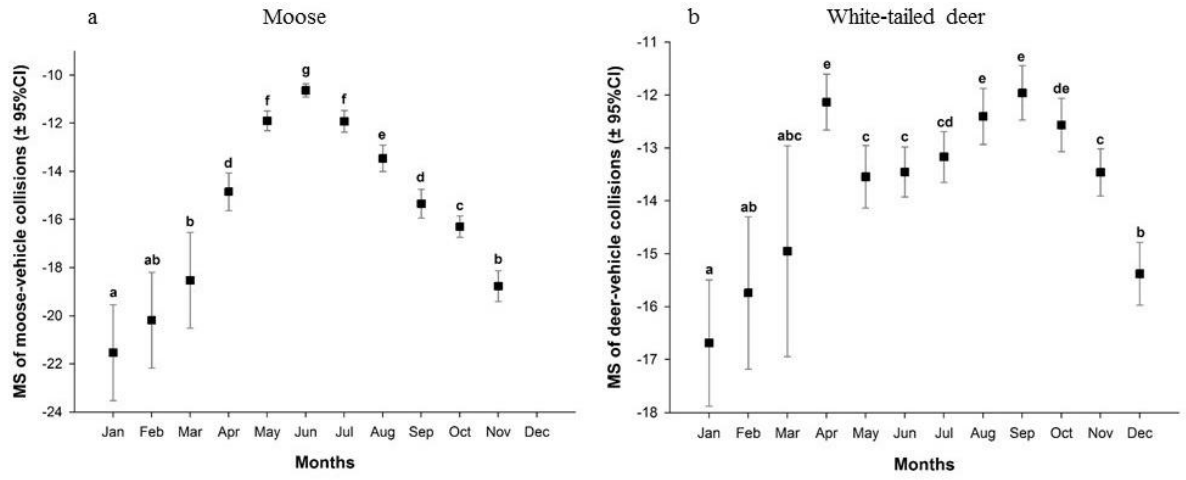

Figure 1. Mean squares (MS) of moose collisions (a, n=198) and white-tailed deer collisions (b, n=252) per months (± 95% CI). No collisions were registered in December for moose thus explaining the lack of result for that month. Months that share the same letter are not significantly different from each other.

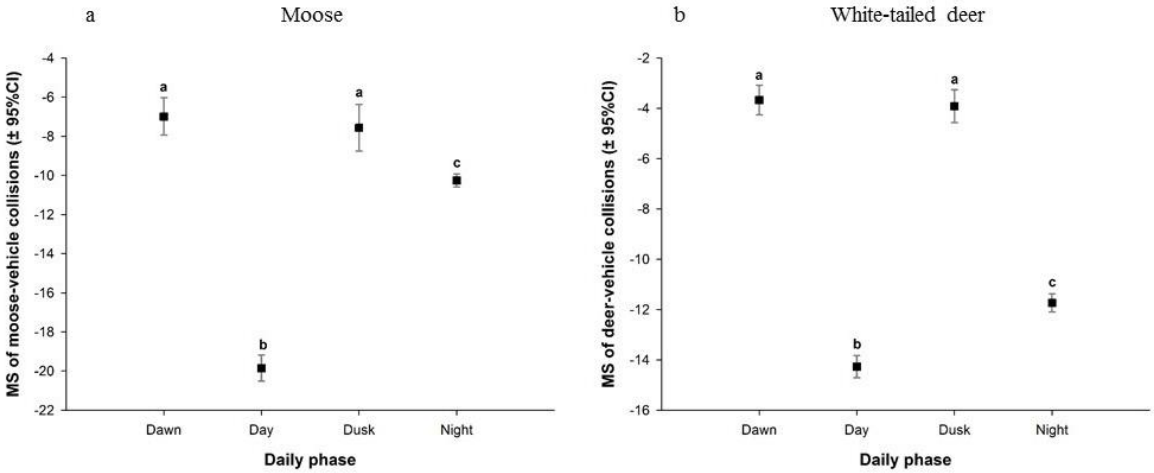

Figure 2. Mean squares (MS) of moose collisions (a, n=198) and white-tailed deer collisions (b, n=252) for each daily phases (± 95% CI). Daily phases that share the same letter are not significantly different from each other.

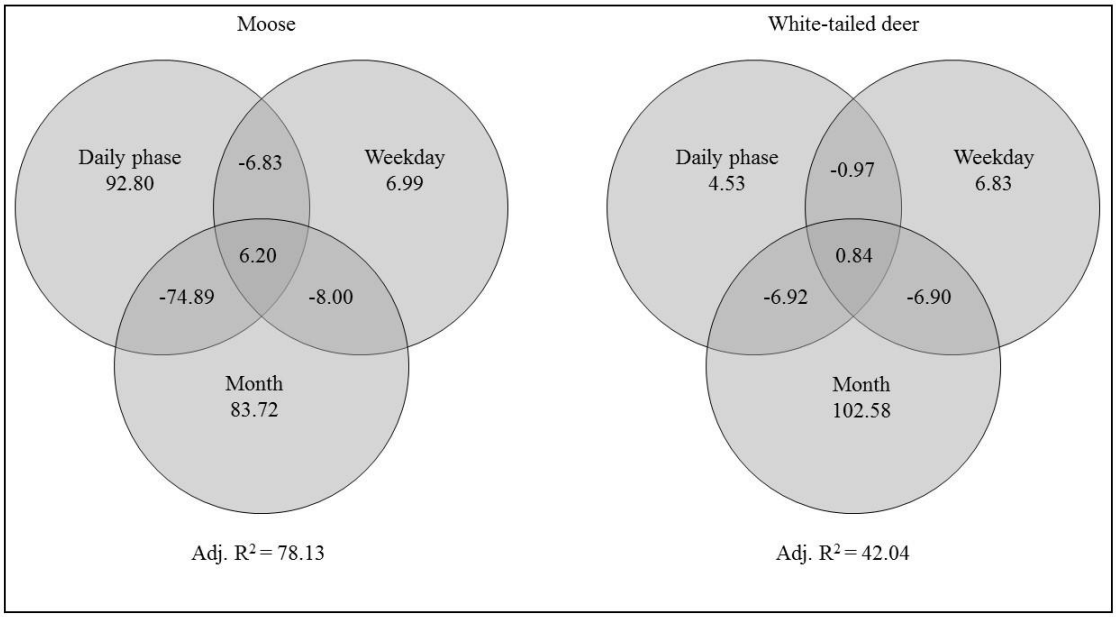

Figure 3. Respective proportions of explained variance (based on adjusted R^2) for effect of month, weekday and daily phase on temporal distribution of moose-caused collisions and deer-caused collisions. Adjusted R^2 (at the bottom) represents the proportion of variance explained by the complete model.

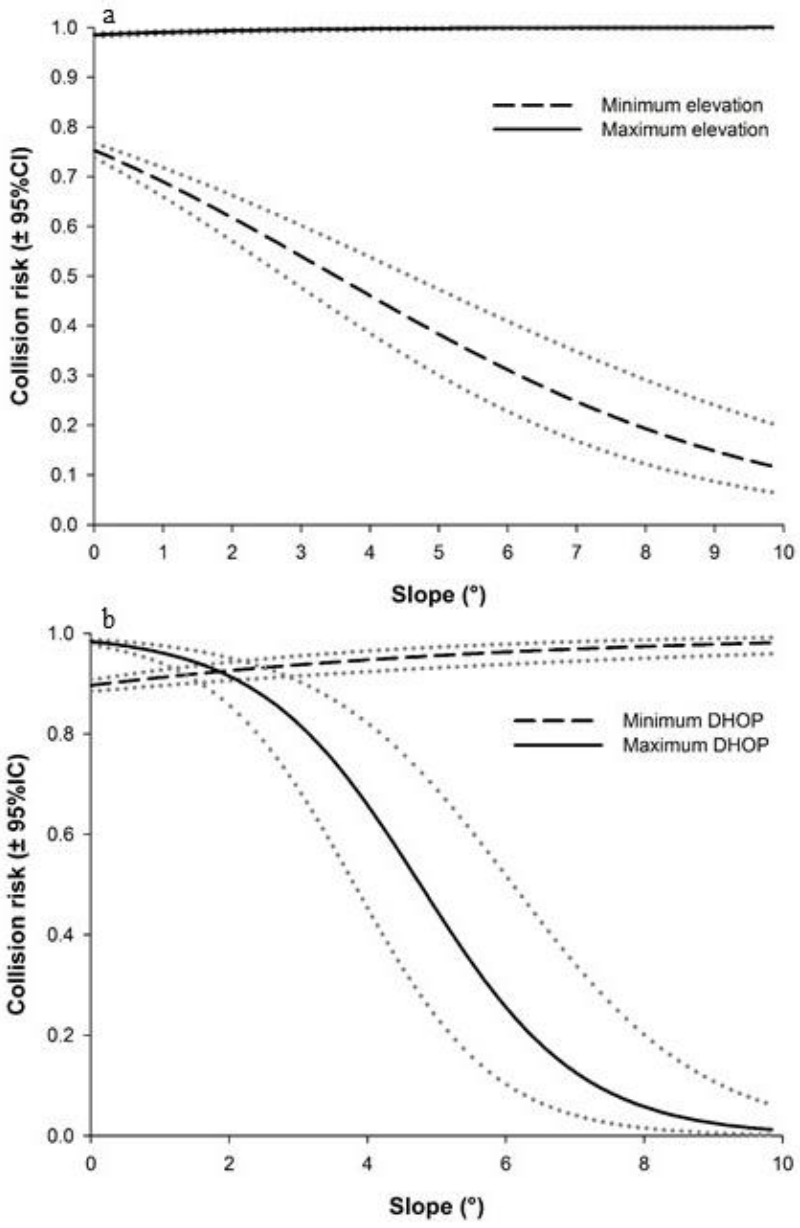

Figure 4. Graphic representation of the effect of the interaction between slope and elevation (a) and between slope and DHOP (b) on the moose-vehicle collision risk on the 85/185 highway situated in southeastern Québec (Canada) from 1990 to 2015. Dotted lines represent 95% CI.

Table 1. Description of landcover types based on numerical 1: 20,000 forest cover maps.

Landcover type	Description
Young clearcuts	0-5 years old clearcuts, all cover types
Old clearcuts	6-20 years old clearcuts, all cover types
Regenerating stands	21-40 years old stands, all cover types
Immature stands	41-80 years old stands, all cover types
Mature deciduous stands	> 80 years old deciduous stands
Mature coniferous stands	> 80 years old coniferous stands
Natural disturbances	0-20 years old fires and insects outbreaks
Wetlands	Bog, fens and marshes
Water bodies	Lakes and rivers
Human	Heavily disturbed habitats by anthropogenic activities
Others	Polygons which did not fit any of the previous criterion

Table 2. Conditional logistic regression candidate models for moose-caused collisions spatial analysis on the 85/185 highway situated in southeastern Québec (Canada) from 1990 to 2015 (n=155). The most parsimonious model is shown in bold.

Model	*k*	*n*	ΔBIC
Luminosity + Sinuosity + Daily rain	3	155	43.28
Maximum daily temperature + Daily rain	2	155	47.30
Forest cover + Distance to a High Occurrence Probability patch (DHOP)	9	155	50.12
DHOP + Proportion of wetlands	2	155	37.79
Slope + Elevation + DHOP + DHOP*Slope + Elevation*Slope	**5**	**155**	**0.00**
Distance to wintering ground + Distance to salt pool	2	155	31.45
Complete	17	155	66.08

Table 3. Conditional logistic regression candidate models for white-tailed deer-caused collisions spatial analysis on the 85/185 situated in southeastern Québec (Canada) highway from 1990 to 2015 (n=168). The most parsimonious model is shown in bold.

Model	*k*	n	ΔBIC
Luminosity + Sinuosity + Daily rain	3	168	10.34
Daily maximum temperature + Daily rain	2	168	11.18
Landcover type + DHOP	9	168	34.56
DHOP	1	168	6.95
Proportion of coniferous mature stands+ Proportion of habitat disturbed by man	2	168	2.79
Slope + Elevation	2	168	10.02
Slope + Elevation + Slope*elevation	3	168	14.75
Slope + Elevation + Elevation2	3	168	14.69
Distance to wintering ground + Distance to salt pool	2	168	11.81
Sinuosity + Proportion of coniferous mature stands	**2**	**168**	**0.00**
Complete	17	168	53.74

Table 4. Coefficients (β) and 95% confidence interval of the most parsimonious model describing collision risk implicating moose on the 85/185 highway situated in southeastern Québec (Canada) from 1990 to 2015 Coefficients for which the 95% CI did not overlap zero had a significant effect on the collision risk.

	β	[lower: upper 95% CI]
Slope	-0.33815	[-0.6120: -0.0640]
Elevation	0.00867	[0.0050: 0.0120]
DHOP	0.00051	[0.0001: 0.0009]
Slope*DHOP	-0.00027	[-0.0003: -0.0002]
Slope*Elevation	0.00209	[0.0010: 0.0030]

Table 5. Coefficients (β) and 95% confidence interval of the most parsimonious model describing collision risk implicating white-tailed deer on the 85/185 highway situated in southeastern Québec (Canada) from 1990 to 2015. Coefficients for which the 95% CI did not overlap zero had a significant effect on the collision risk.

	β	[lower: upper 95% CI]
Sinuosity	1.5255	[0.7500: 2.3010]
Proportion of mature coniferous stands	2.5237	[1.5410: 3.5060]

SUPPLEMENTARY MATERIAL 1. MOOSE RESOURCE SELECTION FUNCTION (RSF)

We built the RSF for moose using data from 20 moose located in the Témiscouata region (southeastern Québec, Canada). Twenty adult moose (2 males and 18 females) were captured and collared (GPS/Iridium Vectronic Vertex Lite 3D, Keswick, Ontario, Canada) during winter 2017, but 5 were harvested by sport hunters in fall 2017. Captures and handling of study animals were approved by the Animal Welfare Committee (according to the guidelines of the Canadian Council on Animal Care) of the Université du Québec à Rimouski (certificates #CPA-68-17-183). An annual home range was delineated for each individual moose using a 95% Minimum Convex Polygon (MCP). GPS locations of each moose were then compared to the same number of random locations distributed within the home range boundaries using a mixed effects logistic regression.

Variables included in the RSF models were land-cover types, slope, elevation and distance to the nearest road and nearest water body. A decay distance transformation ($e^{-\alpha/d}$; Carpenter *et al.* 2010) with an alpha value of 50 was used to attenuate the influence of an increasing distance from roads and plateaud at a distance of 500 m. Variance Inflation Factor (VIF) and Condition Index were calculated to assess multicollinearity among variables. We pooled some habitat categories that had similar use/availability ratios in order to reduce the number of variables (k) in the model: water bodies were then grouped with wetlands, young clearcuts with old clearcuts and natural disturbances with regenerating stands. Mixed effects logistic regressions were used to identify the most parsimonious model and the collar ID was used as a random effect. Three candidate models were built to illustrate the different hypotheses related to habitat, topography or distance to the nearest road and interactions between those variables and the most parsimonious model was chosen using the BIC (Table S1).

This model contained land-cover types and distance to the nearest road (Table S1). Deciduous mature stands, water bodies, wetlands and "other" habitats were avoided by moose while immature stands and 0-20 year old clearcuts were selected (Table S2). Habitats far from roads were also selected. We assessed the robustness of this model using a k-fold

cross-validation (Boyce *et al.* 2002) in which the model was built using 75% of the dataset and validated against the remaining 25%, an operation repeated 49 times (i.e. 50 iterations). The most parsimonious model validation was robust (r_s = 90.63 ± 3.27 % (SD).

Table S1. Logistic regression candidate models built to explain relative occurrence probabilities of moose in the Rivière-du-Loup and Temiscouata regions, southeastern Quebec, Canada (n = 13). The most parsimonious model is shown in bold.

Model	k	n	ΔBIC
Habitat categories[1]	9	13	932
1 + Distance to the nearest road	**10**	**13**	**0**
2 + Squared distance to the nearest road	11	13	373

[1] Coniferous mature stands were used as the reference category in all RSF models.

Table S2. Coefficients (β) and 95% confidence interval of the most parsimonious model describing probability occurrence of moose in the Rivière-du-Loup and Temiscouata regions, southeastern Quebec, Canada. Coefficients for which the 95% CI did not overlap zero had a significant effect on the habitat selection patterns.

	β	[lower: upper 95% CI]
Intercept	-0.739	[-0.806: -0.672]
Deciduous mature stands	-0.282	[-0.329: -0.235]
Water bodies and wetlands	-1.252	[-1.405: -1.099]
Other	-0.456	[-0.542: -0.370]
Immature stands	0.341	[0.284: 0.398]
0-20 year old clearcuts	0.202	[0.158: 0.24512]
Natural disturbances and regenerating stands	0.024	[-0.027: 0.075]
Distance to nearest roads	0.94	[0.879: 1.001]

SUPPLEMENTARY MATERIAL 2. WHITE-TAILED DEER RESOURCE SELECTION FUNCTION

We calculated the resource selection function for white-tailed deer using data from Lesage *et al*. (2000) in which deer were captured and fitted with VHF collars. Deer were captured using Stephenson box traps in the Pohenegamook wintering area (PWA) from 1994 to 1997 and the Lake Temiscouata wintering range (LTWA) from 1994 to 1995 following standard techniques approved by the Animal Welfare Committee of the Université Laval. A total of 100 deer were captured throughout the study period; 38 immatures (16 males and 22 females) and 41 adult (18 males and 23 females) in the PWA and 12 immatures (4 males and 8 females) and 9 adults (2 males and 7 females) in the LTWA. Deer locations were estimated by triangulation with a GPS fixed station and the LOCATE II software (Pacer, Truro, N.S., Canada; Nams 1990). The real deer locations were compared to the same number of random locations in the entire study area based on habitat characteristics with a logistic regression.

Variables included in the models were habitat categories, slope, elevation and distance to the nearest road and nearest water body. The habitat categories were the same as mentioned earlier (see Methods section). Slope and elevation variables were contextualised in 500-m buffer zones around each locations.VIF and Condition Index were calculated to assess collinearity among variables. Logistic regressions were used to identify the most parsimonious model. Five candidate models were built based on different hypotheses related to habitat, topography or distance to the nearest road and interactions between those variables at the population level. The most parsimonious model was identified using the BIC (Table S3).

The most parsimonious model for deer contained habitat categories, slope, elevation, squared elevation, distance to the nearest road and nearest water body. This model suggest that water bodies and "other" habitats were avoided but old cuts, young cuts, natural disturbances and mature coniferous stands were selected, as were higher relative elevation and slope (Table S4). Habitats near water bodies and roads were also selected. The relation between the elevation and the squared elevation showed that deer selected habitats in intermediate elevations. We assessed the robustness of this model using a *k*-fold cross-

validation (Boyce *et al.* 2002) in which the model was tested on 25% of the complete dataset during 50 iterations. The cross-validation classified the outcome of the model with success in 95.22% (SD 2.77) of the cases.

Table S3. Logistic regression candidate models built to explain relative occurrence probabilities of white-tailed deer in the Rivière-du-Loup and Temiscouata regions, southeastern Quebec, Canada (n = 3 042). The most parsimonious model is shown in bold.

Model	k	n	ΔBIC
Habitat categories[1]	10	3042	205.33
1 + Topography	12	3042	113.41
1 + Distance to the nearest road + Distance to the nearest water body	12	3042	143.06
3 + Topography	14	3042	59.20
4 + Elevation + Elevation^2	**15**	**3042**	**0.00**

[1] Regenerating stands were used as the reference category in all RSF models.

Table S4. Coefficients (β) and 95% confidence interval of the most parsimonious model describing probability occurrence of white-tailed deer in the Riviere-du-Loup and Témiscouata regions situated in southeastern Québec (Canada) in 2017. Coefficients for which the 95% CI did not overlap zero had a significant effect on the habitat selection patterns.

	β	[lower: upper 95% CI]
Intercept	-1.117	[-1.570: -0.664]
Mature deciduous stands	0.195	[-0.045: 0.436]
Water	-2.419	[-3.141: -1.697]
Other	-0.708	[-0.959: -0.458]
Immature stands	-0.017	[-0.239: 0.205]
Old cuts	0.830	[0.575: 1.084]
Young cuts	0.677	[0.362: 0.992]
Natural disturbances	0.792	[0.468: 1.116]
Wetlands	-0.457	[-1.002: 0.089]
Mature coniferous stands	0.359	[0.074: 0.643]
Human	-0.310	[-0.842: 0.222]
Distance to nearest road	-0.554	[-0.868: -0.24]
Distance to nearest water body	-0.292	[-0.377: -0.207]
Elevation	9.406	[6.645: 12.168]
Elevation^2	-19.249	[-23.964: -14.534]
Slope	0.116	[0.092: 0.14]

CHAPITRE 2
VALIDATION DES MODÈLES DE CONNECTIVITÉ FONCTIONNELLE : LE TALON D'ACHILLE DE LA CARTOGRAPHIE DE LA CONNECTIVITÉ DU PAYSAGE

Cet article sera soumis dans la revue internationale révisée par les pairs *Landscape and Urban Planning* à l'automne 2018.

2.1 RÉSUMÉ EN FRANÇAIS DU DEUXIÈME ARTICLE

La modélisation de la connectivité fonctionnelle dans les paysages perturbés est l'un des domaines d'expertise en croissance en écologie du paysage, et plusieurs équipes ont proposé différentes méthodes permettant d'évaluer cette connectivité pour un grand nombre d'espèces. Cependant, très peu ont validé empiriquement l'efficacité de tels modèles pour distinguer les corridors réels des corridors théoriques. Les modèles non validés ou ceux basés sur la connectivité structurelle conduisent souvent à des décisions d'aménagement inappropriées ou inefficaces. De plus, la validation pourrait potentiellement révéler que la connectivité fonctionnelle diffère selon l'espèce étudiée ou l'échelle spatiale. Dans cette étude, nous avons comparé empiriquement différente méthodes de validation pour deux modèles de connectivité fréquemment utilisés appliqués à deux espèces de cervidés (i.e. l'orignal *Alces americanus* et le cerf de Virginie *Odocoileus virginanus*) durant un projet d'élargissement de la route. Pour les deux espèces, nous avons construit des cartes de connectivité fonctionnelle en utilisant *CircuitScape* (un modèle basé sur les circuits) et *LinkageMapper* (un modèle de chemins de moindres coûts). Nous avons ensuite validé ces modèles empiriquement à l'aide de quatre métriques différentes, i.e. la densité de collisions routières impliquant les cervidés, la distance au ravage le plus proche et le taux de détection calculé avec des caméras automatiques et des trappes à sable. La validation a été effectuée à différentes échelles spatiales (150, 500, 1000, 1500, 2000 et 2500m). Le modèle basé sur les circuits performait mieux pour identifier les corridors de connectivité fonctionnelle pour les deux espèces. La force de la validation différait grandement entre les quatre métriques utilisées et entre les échelles spatiales auxquelles la corrélation entre la connectivité et les données a été évaluée. Notre étude souligne l'importance de valider les modèles de connectivité fonctionnelle afin de fournir les meilleurs outils de prise de décision.

Mots clés : cerf de Virginie (*Odocoileus virginianus*), cervidés, connectivité fonctionnelle, écologie du paysage, écologie routière, orignal (*Alces americanus*), validation

2.2 VALIDATION OF FUNCTIONAL CONNECTIVITY MODELING: THE ACHILLES' HEEL OF LANDSCAPE CONNECTIVITY MAPPING

Abstract

Modeling functional connectivity in altered landscapes is one of the growing fields of expertise in landscape ecology, and many research teams have proposed different methods to evaluate it for a wide range of species. However, very few have empirically validated the efficiency of such models in discriminating real corridors from theoretical ones. Models that are not validated or those only based on structural connectivity could result in inefficient management decisions. Moreover, validation could potentially reveal that functional connectivity differs between focal species and spatial scales. Here we empirically compared different validation methods for two commonly used connectivity models applied to two cervid species (i.e. moose *Alces americanus* and white-tailed deer *Odocoileus virginianus*) during a road enlargement project. For both species, we built functional connectivity maps using *CircuitScape* (circuit-based model) and *LinkageMapper* (least-cost path model). We then validated them empirically using four different metrics, i.e. density of cervid-vehicle collisions, distance to the nearest wintering ground and detection rate calculated with automated cameras and with sand traps. Validation was carried out at various spatial scales (150, 500, 1000, 1500, 2000 and 2500m). The circuit-based models performed better at identifying functional corridors of connectivity for both species. Validation strength differed greatly between the four metrics used and between the spatial scale at which the correlation between connectivity and data was assessed. Our study emphasizes the importance of validating functional connectivity models to provide the best decision-making tools.

Keywords : cervids, functional connectivity, landscape ecology, moose (*Alces americanus*), road ecology, validation, white-tailed deer (*Odocoileus virginianus*)

INTRODUCTION

The alteration of natural habitats, caused by mining industry (Sasaki *et al.* 2015), forest exploitation (Layton-Matthews *et al.* 2018) or urban development (Liu *et al.* 2016), is a major driver of landscape change worldwide (Barnosky *et al.* 2012; Haddad *et al.* 2015). All these types of anthropogenic disturbance induce loss and fragmentation of natural habitats (Barnosky *et al.* 2012; Haddad *et al.* 2015). Habitat loss is closely associated with fragmentation (Fahrig 2003), as the drivers of landscape alteration often induce both simultaneously, making it challenging to distinguish their respective effects (St-Laurent *et al.* 2009; Hadley & Betts 2016). By increasing loss and fragmentation of natural habitats, resources can be aggregated in one place or distributed heterogeneously across the landscape (Fahrig 2003; Banks *et al.* 2007). Animals are then compelled to move from one patch to another to find all the resources needed, exposing them to a riskier matrix in less suitable habitat and consequently increasing the risk of mortality (Fahrig

2002, 2003). Generally, the decrease in the amount of habitat and the associated increase of fragmentation are the starting points for a decrease in landscape connectivity (Crooks & Sanjayan 2006; Haddad *et al.* 2015). Recently, Fahrig (2017) reviewed the effects of fragmentation per se on several facets of wildlife ecology and showed that in 76% of the studies consulted, fragmentation (per se) had a positive effect on wildlife populations as species richness increased with fragmentation. This literature review laid the foundationsto the hypothesis that fragmentation can improve landscape connectivity by creating stepping-stones of good habitat in the matrix (Fahrig 2017).

Studying landscape connectivity requires distinguishing the different types of connectivity, a concept that is often wrongly used or poorly defined (Tischendorf & Fahrig 2000). Taylor *et al.* (1993) defined landscape connectivity as "*the degree to which landscape facilitates or impedes movement among resource patches*". Landscape connectivity is thus composed of two different facets, namely structural connectivity and functional connectivity (Baguette & van Dyck 2007). Structural connectivity is defined as the level at which two habitat patches are physically connected. On the other hand, some abiotic or biotic factors may make this connexion unsuitable for some species, resulting in lower connectivity for a given species than what is suggested by the structural connectivity (Tischendorf & Fahrig 2000; Bélisle 2005). The resulting level of connexion between suitable habitat patches is called functional connectivity. Indirect habitat loss is observed when a habitat is physically present but is rendered unusable (or less usable) or unattractive (or less attractive) (*sensu* Polfus *et al.* 2011) by the means of several stressors (*e.g.* roads: Kramer-Schadt *et al.* 2004; sound pollution: Parris 2015; human presence: Lesmerises *et al.* 2018). Consequently, functional habitat loss and functional connectivity are as closely related as habitat loss and fragmentation are. Furthermore, Baguette & van Dyck (2007) noted that structural connectivity should be regarded from a landscape perspective while functional connectivity should be regarded from the organism's point of view.

Early on, Taylor et al. (1993) identified connectivity as a key factor in population dynamics. In addition, Dupras *et al.* (2016) noted a steep decrease in connectivity from 1981 to 2010 in a metropolitan region, resulting in an urgent need to model landscape (Beier & Noss 1998). Many researchers have recently developed connectivity models (Merrick & Koprowski 2017; Albert *et al.* 2017; Khosravi *et al.* 2018), but these models are rarely validated using empirical, independent data (e.g. Walpole *et al.* 2012; Koen *et al.* 2014; Marrotte *et al.* 2017), raising doubts and concerns

regarding their use to orient landscape management. In addition, not all metrics of structural connectivity can provide clear insights about functional connectivity (Calabrese & Fagan 2004). For example, Winfree *et al.* (2005) showed that patch proximity was insufficient to explain animal movements in altered and natural landscapes. Landscape connectivity is also known to be species-specific, as many studies have highlighted various effects of landscape structure on the population dynamics of different sympatric species (Keitt *et al.* 1997; Renjifo 2001; Steffan-Dewenter *et al.* 2002; Uezu *et al.* 2005). Consequently, functional connectivity should be assessed from a species' point of view (Baguette & van Dyck 2007; Vogt *et al.* 2009). It is therefore justified to interpret functional connectivity as the interaction of a species with the landscape in which it evolves (D'Eon *et al.* 2002; Baguette & van Dyck 2007). Given that different species exhibit variable dispersal capacities (D'Eon *et al.* 2002; Vasudev *et al.* 2015), the spatial scale at which connectivity should be studied is therefore variable and depends on the species studied (Lechner *et al.* 2017; Liu *et al.* 2018). Accordingly, functional connectivity must be spatial-scale dependent (Keitt *et al.* 1997; Milanesi *et al.* 2017).

The relationship between connectivity and its effect on animal population dynamics have been studied and demonstrated to various degrees of comprehension (FitzGibbon *et al.* 2007; Awade & Metzger 2008). In addition, connectivity modeling often yields various results, which can be contradictory (Urban *et al.* 2001; Roever *et al.* 2013; Grafius *et al.* 2017; Buderman *et al.* 2018). Some warnings and cautions have been raised, as theory may not always reflect reality (Naidoo *et al.* 2018) and animals may not always be able to make optimal choices as suggested by model outputs (Fahrig 2007). As connectivity modeling is often used to address important issues like disease spread (Algeo *et al.* 2017) and climate change refuges (Morelli *et al.* 2017), it is important to investigate factors influencing connectivity results and model limitations.

Here we modelled functional connectivity using two commonly used softwares, i.e. *CircuitScape* (McRae *et al.* 2008) and *LinkageMapper* (McRae & Kavanagh 2011), in order to identify potential movement corridors for moose (*Alces americanus*) and white-tailed deer (*Odocoileus virginianus*) in a landscape fragmented by a major road enlargement project. We thereafter explored the influence of validation methods to assess the precision of these two frequently used models and the influence of an increasing buffer size (proxy for different spatial scales) on the validation strength.

METHODS

Study area

Our study area is located in the Bas-St-Laurent region, southeastern Québec, Canada, where the 85/185 highway is the main link between the city of Rivière-du-Loup (in the province of Québec) to the New-Brunswick border. This road axis is currently under construction to go from a two-lane provincial road to a four-lane provincial highway. Wildlife – vehicle collisions are a major public safety threat on the 85/185 highway, involving mostly moose and deer (see Chapter 1 of this thesis). Modeling and validating potential crossing corridors on that highway is therefore a crucial step to improve public safety and efficiently plan mitigation measures.

We took advantage of this road enlargement project to study the functional connectivity of the landscape and the permeability of the road axis in a wildlife-vehicle collision and public safety context. The study area is located in a region representative of the balsam fir (*Abies balsamea*) – yellow birch (*Betula alleghaniensis*) domain. Dominant tree species are balsam fir, white spruce (*Picea glauca*), yellow birch, white birch (*B. papyrifera*) and northern white-cedar (*Thuja occidentalis*) (Robitaille & Saucier 1998). The large- and medium-sized mammal species encountered in this region are moose, white-tailed deer, black bear (*Ursus americanus*), coyote (*Canis latrans*), red fox (*Vulpes vulpes*) and Canada lynx (*Lynx canadensis*). Moose densities are amongst the highest in eastern Canada as wolves (*Canis lupus*), its main predator, have been extirpated from the south shore of the St. Lawrence River ~150 years ago; consequently, local densities reached 0.5 moose/km^2 (MFFP 2016) with regional peaks at 2.3 moose/km^2 (Ross *et al.* 2014),. This region is characterised by a mean elevation of 290m and low rolling hills (slopes of 7% on average) (Robitaille & Saucier 1998). Mean annual temperature is 2.5°C with annual precipitations ranging from 900 to 1000mm of which 35% falls as snow. Forested habitats dominate the landscape (~85%), but agriculture is also common (~15%). Several small rural and agricultural villages are distributed throughout the entire region (Robitaille & Saucier 1998). Annual Average Daily Traffic (AADT) on the 85/185 highway varies from 840 to 12,600 cars day^{-1} km^{-1} with a mean value of 7 724 cars day^{-1} km^{-1}.

Geomatic data

We used a 1: 20,000 numerical ecoforest map published by the Ministère des Forêts, de la Faune et des Parcs (hereafter MFFP) and updated annually to integrate natural and anthropogenic disturbances. Land cover polygons were classified into 11 categories: 0-5 year-old clearcuts, 6-20 year-old clearcuts, 21-40 year-old regenerating stands, 41-80 year-old forest stands, >80 year-old mature deciduous stands, > 80 years-old mature coniferous stands, 0-20 year-old natural disturbances (fires and insect outbreaks), wetlands, water bodies, human (habitats heavily disturbed by anthropogenic activities) and others (polygons that did not match previous criteria). We used numerical 1: 20,000 maps of roads and topography published by the MFFP to build a digital elevation model and extract elevation and slope.

Landscape connectivity analyses

We used two different methods to evaluate landscape connectivity in our study area: *CircuistScape* (v4.0.3; McRae *et al.* 2008) and *LinkageMapper* (v1.0.9; McRae & Kavanagh 2011). *CircuitScape* employs graph and electrical circuit theories to map connectivity corridors as connections of an electrical circuit. To do so, *CircuitScape* requires two rasters, the first representing the core areas of suitable habitats to be connected (i.e. the nodes) and the other showing the resistance values for the landscape studied. Connectivity corridors are then identified as the corridors with higher current values between nodes.

LinkageMapper is an ArcGIS extension allowing the use of various wildlife habitat connectivity analysis tools. As for *CircuitScape, LinkageMapper* uses core areas and movements resistance rasters. This tool uses the least-cost path theory (Adriaensen *et al.* 2003) to identify corridors where habitat characteristics facilitate or hinder movement.

Resistance rasters for each species were derived from a Resource Selection Function (hereafter referred to as RSF; Manly *et al.* 2002), which is an appropriate method when the study area is a semi-continuous forested matrix without highly unfavorable habitats (Galpern *et al.* 2011). For moose, the RSF was built using moose telemetry locations collected in the Témiscouata region (included in our study area), where 20 moose (2 males and 18 females) were captured and fitted with GPS collars during the winter of 2017 (St-Laurent, *unpublished data*) (Figure S1). For deer, the RSF was built using deer telemetry locations gathered on 100 deer collared with VHF collars (see Lesage *et al.* 2000 for more details) (Figure S1). A total of 100 deer were captured

using Stephenson traps in the Lake Témiscouata wintering area (LTWA) in 1994 and 1995 and in the Pohénégamook wintering area (PWA) from 1994 to 1997. In the PWA, 38 of the collared deer were immatures (16 males and 22 females) and 41 were adults (18 males and 23 females), while in the LTWA, 12 were immatures (4 males and 8 females) and nine were adults (2 males and 7 females).

Independent variables used to build the moose RSF were 11 land-cover types and distance to the nearest road. Topographic variables (elevation and slope) were not included in the model as the degrees of freedom were limited (See Suppl. Mat. 1). Variables included in the deer RSF were land-cover types, slope, elevation, distance to the nearest water body and distance to the nearest road (See Suppl. Mat. 2). A negative linear transformation was applied to RSF scores (1 – RSF score; as described by Chetkiewicz & Boyce 2009) and multiplied by 100, which we subjectively interpreted as landscape resistance (see Beier *et al.* 2008*).* Impermeable barriers were assigned the maximum resistance value of 1000, and an intermediate resistance value of 500 was applied to a 500-m buffer zone around buildings. We also defined the resistance for water bodies at a value of 300. Roads resistance was adjusted based on the average annual daily traffic as lower traffic volume was suspected to be more permeable. To do so, we created four categories of traffic volume: less than 1000, from 1000 to 4999, from 5000 to 9999 and more than 10,000 (Table 1).

We built rasters of core areas (interpreted as circuit "nodes") for each species using relative occurrence probability maps based on their respective RSF. For both species, we selected the 2.5% highest ranked habitats that had a minimum area of 150 ha for moose and 80 ha for deer. The minimum area considered differed between species based on average home range size as moose have larger home ranges than deer. We did not use a buffer zone around our study area, as opposed to Koen *et al.* (2014), because our main focus was to characterize functional connectivity in the center of our area; thus, eliminating the bias in the periphery of our area was not necessary.

Validation approaches

The validation process consisted in the evaluation of the strength of the relationship between the two connectivity models and four independent variables obtained through field surveys. The four variables were cervid-vehicle collision densities, distance to the nearest wintering ground and detection rate by two types of devices. We used wintering grounds as a proxy for cervid densities as we expected them to move toward wintering grounds in late fall and from

it during early spring. We used collisions data from the Société de l'Assurance Automobile du Québec (hereafter SAAQ) to build a database of wildlife-vehicle collisions involving moose and white-tailed deer on the 85/185 road axis from 1990 to 2015. The driver involved in the accident reported each individual collision to the SAAQ and some important variables were compiled: the date of the collision, the species and the number of animals involved in the collision, as well as several variables referring to injuries to the driver and passengers and damages to the car. We then divided the dataset in two parts based on species involved and mapped their distribution with ArcMap 10.1 (ESRI Inc., Redlands, California). We also used the location of moose and white-tailed deer wintering grounds assessed by aerial surveys (MFFP 2016). Cervid-vehicle collision densities and distance to the nearest wintering ground were calculated for each 1-km segment of the road. The middle point of the road segment was used to measure the distance to the nearest wintering ground. We randomly distributed 80 automated cameras and 59 sand traps in a 1-km buffer zone around the road axis during the summer of 2017 in order assess animal movement. We visited each device (*i.e.* sand trap and automated camera) every 2 weeks to change memory cards from cameras, retrieve photos and reset the sand traps (erasing the tracks and smoothing the sand with a rake). We calculated the detection rate by species for each device by dividing the number of animals detected by the number of days that the device was in operation.

The strength of the relationship linking each variable to the connectivity models was assessed via a linear regression for collisions densities, a Pearson's correlation for distance to the wintering areas and a Spearman's rank correlation for both detection rates. Spearman's rank correlation (based on 10 bins) was preferred over a Pearson's correlation to deal with the high variability in both camera trap and sand trap detection rates. We calculated the average connectivity value from both models in a buffer zone centered on the middle of each 1-km segment of the 85/185 highway as well as around camera trap and sand trap locations. We also evaluated the effect of an increasing buffer radius (150, 500, 1000, 1500, 2000, and 2500m) on the strength of the relationships. These buffer zones were used to contextualise functional connectivity around each camera and sand trap location and the middle of each 1-km road segment. We used this method to determine the spatial scale at which our four validation variables were most affected by functional connectivity.

RESULTS

Connectivity modeling

Connectivity modeling patterns differed between *CircuitScape* and *LinkageMapper* (Figure 1). *CircuitScape* produced more dispersed, sparse and convoluted corridors, while *LinkageMapper* generated more linear connectivity corridors. We obtained an inverse relation between the two methods (as *CircuitScape* maps conductivity and *LinkageMapper* maps resistance) and noted that sites offering a high connectivity were more apparent with *CircuitScape* (Figure 2). When comparing connectivity patterns between the two cervid species, it appears that moose connectivity corridors were more concentrated in the middle of the study area while deer corridors were mainly north of the 185/85 road axis.

Validation

The strength of the validation differed between species, connectivity models, metrics used to validate the models and size of the buffer zone (Table 2). The metrics we used to evaluate the efficiency of the connectivity models varied greatly along the road axis (Figures 3 & 4). For moose connectivity, the variable most correlated with connectivity was the detection rate by cameras ($p < 0.05$, Spearman's $\rho = 0.83$) when using *CircuitScape* and collision density when using *LinkageMapper* ($F_{(2,97)} = 30.72$, $p < 0.05$, adj.-$R^2 = 0.38$) (Table 2). For deer, the detection rate obtained from sand traps correlated most with connectivity when using *CircuitScape* ($p < 0.05$, Spearman's $\rho = -0.92$), but distance to the nearest wintering ground correlated most when using *LinkageMapper* ($p < 0.05$, Pearson's $r = 0.32$) (Table 2). We assessed the influence of buffer radius on correlation strength for the different models for both cervids (Figure 5). The correlation between connectivity values and detection rate by camera varied slightly for moose depending on buffer size; the highest correlations ($p < 0.05$, Spearman's $\rho = 0.83$) were obtained using buffer radii of 500, 1000 and 2000m respectively (Figure 5a). In contrast, buffer size had a strong effect on the strength of the correlation between connectivity values and detection rate by sand traps for deer (Figure 5b). Correlation strength increased with the buffer radius, and the strongest correlation ($p < 0.05$, Spearman's $\rho = -0.92$) was obtained with a buffer size of 2000m.

DISCUSSION

Connectivity modeling

Connectivity patterns differed at the landscape scale between moose and deer, a finding consistent with results obtained by other studies that showed that connectivity is a species-specific landscape characteristic (Steffan-Dewenter *et al.* 2002; D'Eon *et al.* 2002; Uezu *et al.* 2005; Palmer *et al.* 2011). However, some studies found similar connectivity patterns for species sharing comparable habitat requirements (e.g. Lechner *et al.* 2017; Khosravi *et al.* 2018). The different connectivity patterns we noted could be explained by the different movement capacities (Correa Ayram *et al.* 2017) and habitat preferences (Steffan-Dewenter *et al.* 2002) of the studied species.

In Quebec, the main drivers of moose habitat selection are (in decreasing order of importance) predation risk, browse availability and snow depth (Dussault *et al*. 2005a). Due to the extirpation of wolves south of the St. Lawrence River, humans are the main predators of moose in the study area (via sport hunting). This is also the case in the adjacent province of New Brunswick, where habitat conditions are similar with wolves being extirpated (Fryxell *et al.* 1988; Boer 1998). Therefore, we consider that browse availability (both in quantity and in quality; see van Beest *et al.* 2010) is the main driver of moose habitat selection south of the St. Lawrence River where moose are found at very high densities (Leblond *et al*. 2015). In such regions, white-tailed deer face greater predation risks by coyotes (Ballard *et al.* 1999; Whittaker & Lindzey 1999), the second-largest canid in North America, which could explain the different habitat selection patterns and connectivity compared to moose. In fact, predation by coyotes is one of the main limiting factors of white-tailed deer populations in North America due to the reduced survival of neonates (Michel *et al.* 2018). We believe that the difference in habitat selection, associated with the anti-predator strategies of moose and deer (McLoughlin *et al.* 2005; Creel *et al.* 2005; Smolko *et al.* 2018) on the south shore of the St. Lawrence River, could explain the observed differences in functional connectivity.

CircuitScape generated dispersed and convoluted corridors while *LinkageMapper* produced linear corridors. This could be explained by the mathematical theories employed by the models. *LinkageMapper* uses the theory of least-cost paths (Adriaensen *et al.* 2003), which assumes that animals are fully conscious of the entire study area and, therefore, can make the best choice to move from point A to point B (Palmer *et al.* 2011); hence, only one link can be modelled (Moilanen 2011). In contrast, circuit-based models use random walk algorithms and animals can

only perceive the landscape in a 1-cell radius (McRae *et al.* 2008). Therefore, it assumes that animals make a decision at each pixel (Bond *et al.* 2017), leading to different location possibilities for corridors. In addition, least-cost path models are highly sensitive to resistance value attribution (Rayfield *et al.* 2010; Moilanen 2011). This could cause straight-lined corridors to occur more often, especially if the resistance matrix is overly generalized (i.e. resolution does not allow discrimination between high and low resistances) and only low resistance differences are found between habitats (Rayfield *et al* 2010; Koenig & Bender 2018). In the context of a road construction project, connectivity models using *CircuitScape* were initially supposed to be a better option as it allows the identification of pinch points of high connectivity potentially crossing the road. This is especially true when the habitat matrix is homogenously suitable for focal species, as it was the case in our study area. Nevertheless, only the validation of the connectivity corridors could confirm this *a priori* assumption.

The transformation used to convert habitat quality into resistance values could also be an additional factor that may influence the results of connectivity analyses, as suggested by Keeley *et al.* (2016, 2017) and Zeller *et al.* (2018).

Validation

As stated by Simberloff *et al.* (1992), it is important that the corridors of interest are actually being used by wildlife, especially when the aim of the study is to identify corridors where the probability of road crossing by wildlife is high and collision risk could threaten public safety. Otherwise, such an exercise remains theoretical. We were thus expecting more signs of moose and deer presence (*i.e.* higher detection rates and greater collision densities) and/or shorter distances to suitable habitats (*i.e.* wintering grounds) where the connectivity models highlighted a higher functional connectivity. However, the validation process revealed great differences in validation strength between the connectivity values and the validation metrics used.

Collision densities and distance to the nearest wintering ground correlated least with connectivity, suggesting that these two variables were poorly related to connectivity at the spatial scales we investigated. On the other hand, detection rates from cameras and sand traps correlated more strongly with connectivity. Collision risk is not homogeneously distributed along a road axis therefore other factors could be at play, such as driver's capacity to detect and avoid an animal on the road (Rea *et al.* 2018). A low collision density value could be present where animals are able

to cross the road without being hit by a car (Hothorn *et al.* 2012; Thurfjell *et al.* 2015). Therefore, we consider that collision densities might not be the best predictor of functional connectivity, as the strength of our relationship between collision densities and connectivity was quite low, and thus do not recommend using it to validate connectivity models.

The appeal of using distance to the nearest wintering ground appeared mitigated in our study, as this variable might only be relevant during periods when cervids are using those wintering grounds. Cervids from northern regions are known to modify their behavior during winter to seek shelter from deep snow and thus limit their energy expenditure (Sabine *et al.* 2002; Dussault *et al.* 2005a; Lundmark & Ball 2008). To do so, animals may move to wintering grounds that are spatially segregated from their summer ranges (Porter *et al.* 2004; Hurst & Porter 2008), but they can also reduce their movement rate (Dussault *et al.* 2005b). This seasonal difference in space use for cervids could explain why distance to the nearest wintering ground was not a good predictor of functional connectivity in our study, as the connectivity was assessed for the entire year. Distance to the nearest wintering ground could perform better during the snow covered seasons.

Detection rates can reflect animal movements along the road axis, an approach facilitated by the growing use of automated cameras to monitor animal movement (Tobler *et al.* 2008; Kays *et al.* 2011) and estimate local density (Rowcliffe *et al.* 2008). Detection probability by a camera, however, is highly correlated with animal body size (Tobler *et al.* 2008; Lyra-Jorge *et al.* 2008) and, to a lesser extent, speed (or movement rate; Rowcliffe *et al.* 2011), making this method appropriate to monitor large ungulates movements. This could explain the results that we obtained, as detection rates by cameras were strongly correlated with the functional connectivity values of moose. However, we observed a strong negative relationship between deer detection rates by sand traps and deer connectivity, suggesting that connectivity corridors would be located where the detection rates by sand traps were lower, which is counter intuitive. According to Ford *et al.* (2009), there are two important limitations to sand traps: 1) they offer lower confidence in species identification than automated cameras and 2) data quality can degrade due to weather conditions and animal use. We encountered both these problems in the field, as tracks were often unidentifiable due to rain, drought or the overlaying of tracks in the sand. This could explain the non-intuitive relationship between connectivity and sand trap detection rate that we observed for deer.

Although some studies highlighted a greater performance of least-cost paths or cost-weighted distance models (McClure *et al.* 2016; Zeller *et al.* 2018), we observed that models using circuit theory outperformed other models based on our validation, which is supported by other studies (McRae & Beier 2007; Moore *et al.* 2011). Altogether, least-cost path models may not be an appropriate indicator of animal movement for many species (Pullinger & Johnson 2010; Palmer *et al.* 2011; Moilanen 2011) and circuit-based models might be more applicable to various scenarios (McClure *et al.* 2016). However, a combination of the two models could be beneficial in connectivity mapping, as explained by Gangadharan *et al.* (2017), as circuit-based models could be used for broader scale modeling while least-cost path models can be preferred for finer scales.

Spatial scale

Our results highlight the importance of selecting the appropriate spatial scale when validating connectivity models as the strength of the relationship between our modelled connectivity and validation metrics varied with an increasing buffer radius (Figure 5). The interaction between a species and its environment occurs at different scales depending on the species studied (D'Eon *et al.* 2002; Steffan-Dewenter *et al.* 2002). This spatial scale dependency can be explained by the fact that landscape features that are impermeable to some species could be of lesser concern for another (Wheatley & Johnson 2009; Vogt *et al.* 2009; Lechner *et al.* 2017). In fact, spatial scale often influences habitat selection, as different resources may be relevant at different scales (Leblond *et al.* 2010; Zeller *et al.* 2014; 2016). Since resistance rasters are often based on RSFs (Chetkiewicz & Boyce 2008; Pullinger & Johnson 2010; Roever *et al.* 2013), this spatial scale dependency is likely to be transferable to functional connectivity as well.

MANAGEMENT IMPLICATIONS

Our study highlights the importance of validating the accuracy of connectivity models using empirical data and the importance of choosing appropriate validation metrics, a crucial step previously pointed out by Galpern (2011). This prerequisite is supported by the important variation in validation results we obtained depending on the model and the validation metric used, the species studied, and the spatial scale considered. An additional validation step could be to compare connectivity models to null models where the resistance matrix is set to 0 for the entire study area, as described by McClure *et al.* (2016) and applied by Bond *et al.* (2017). Also, updating the

identification of core habitats and assessing resistance values using more recent telemetry data for deer in our study area could be interesting, as our telemetry data were collected in 1997, in a slightly different landscape (from both a compositional and a structural perspectives).

The methods we used to model and validate functional connectivity can be advocated to identify movement corridors that may cause road safety issues in road development projects and to help identify the location of potential mitigation structures (McClure & Ament 2014). They can also be applied using a coarse-scale conservation approach to focus management efforts on connectivity corridors that should be prioritized for a threatened species (Moqanaki & Cushman 2017) or even to maintain a minimum level of connectivity (Hofman *et al.* 2018).

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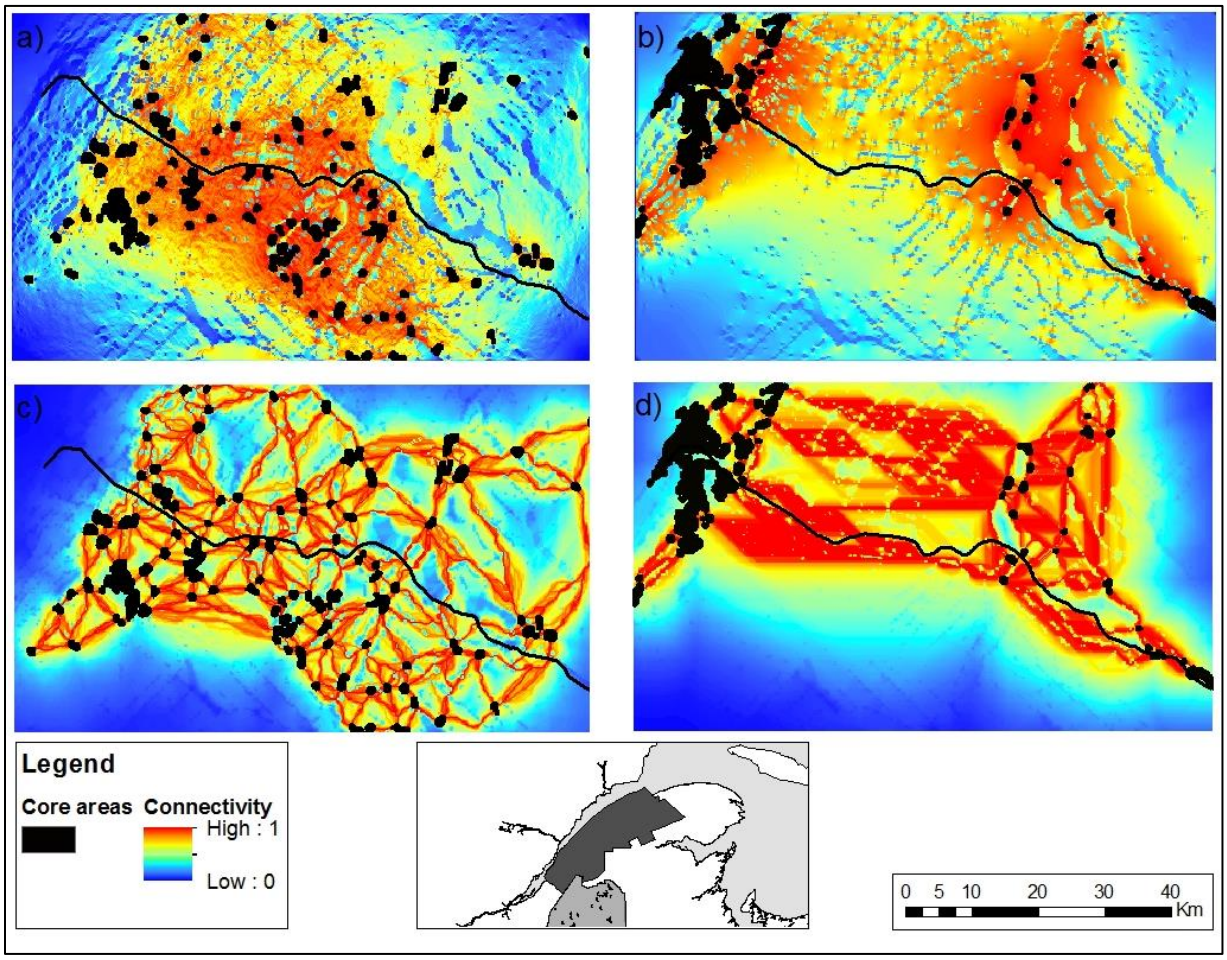

Figure 1. Functional connectivity modeling using CircuitScape for moose (a) and white-tailed deer (b) and using LinkageMapper for moose (c) and white-tailed deer (d) along the 85/185 road axis in southeastern Québec, Canada.

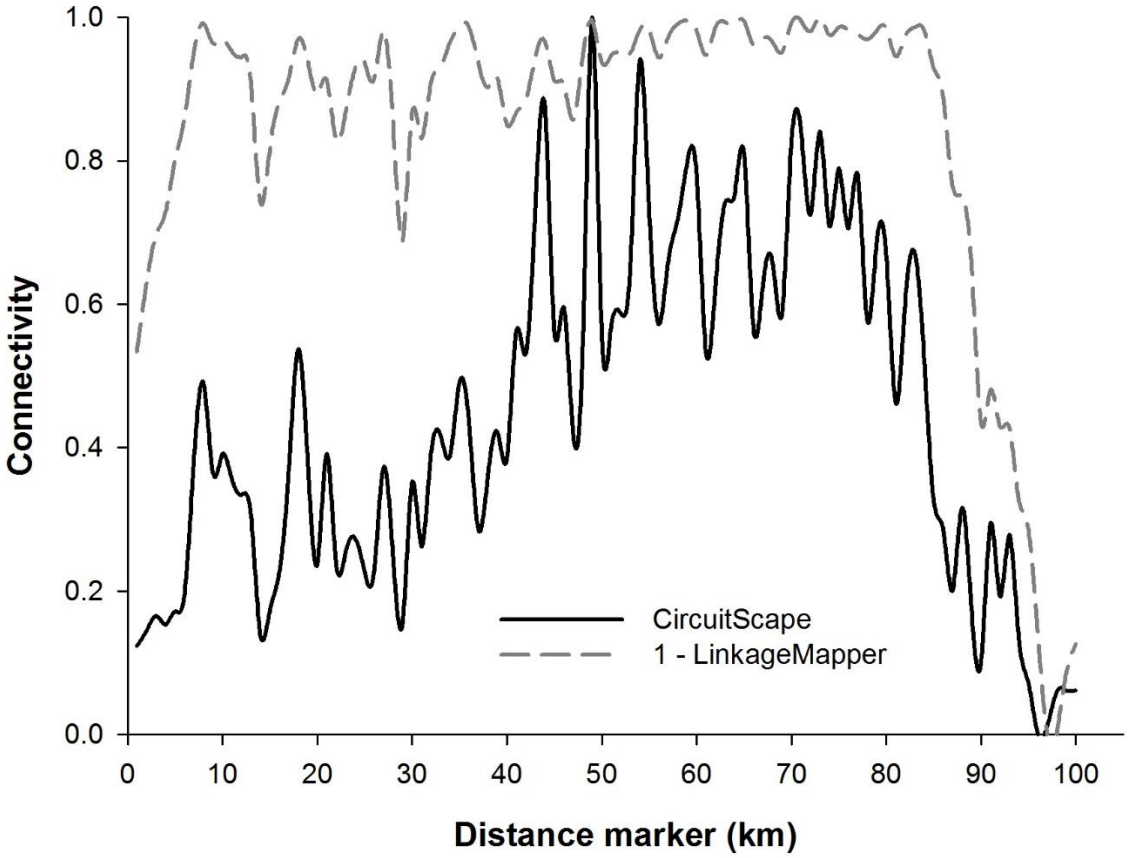

Figure 2. Comparison of moose connectivity values modelled with *CircuitScape* and *LinkageMapper* for each kilometer along the 85/185 road axis in southeastern Québec, Canada.

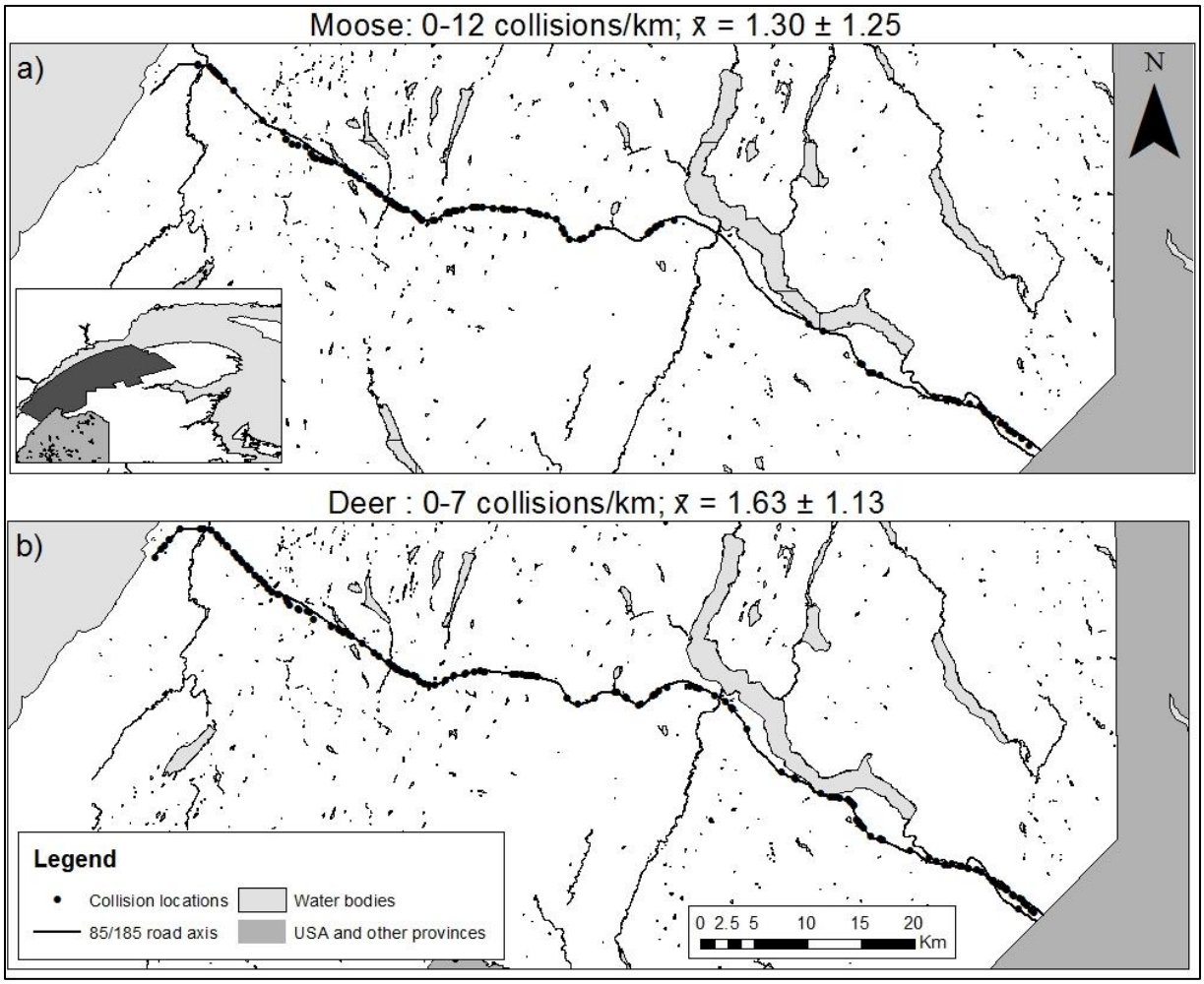

Figure 3. Locations of moose- and white-tailed deer-vehicle collisions on the 85/185 road axis in southeastern Québec, Canada between 1990 and 2015.

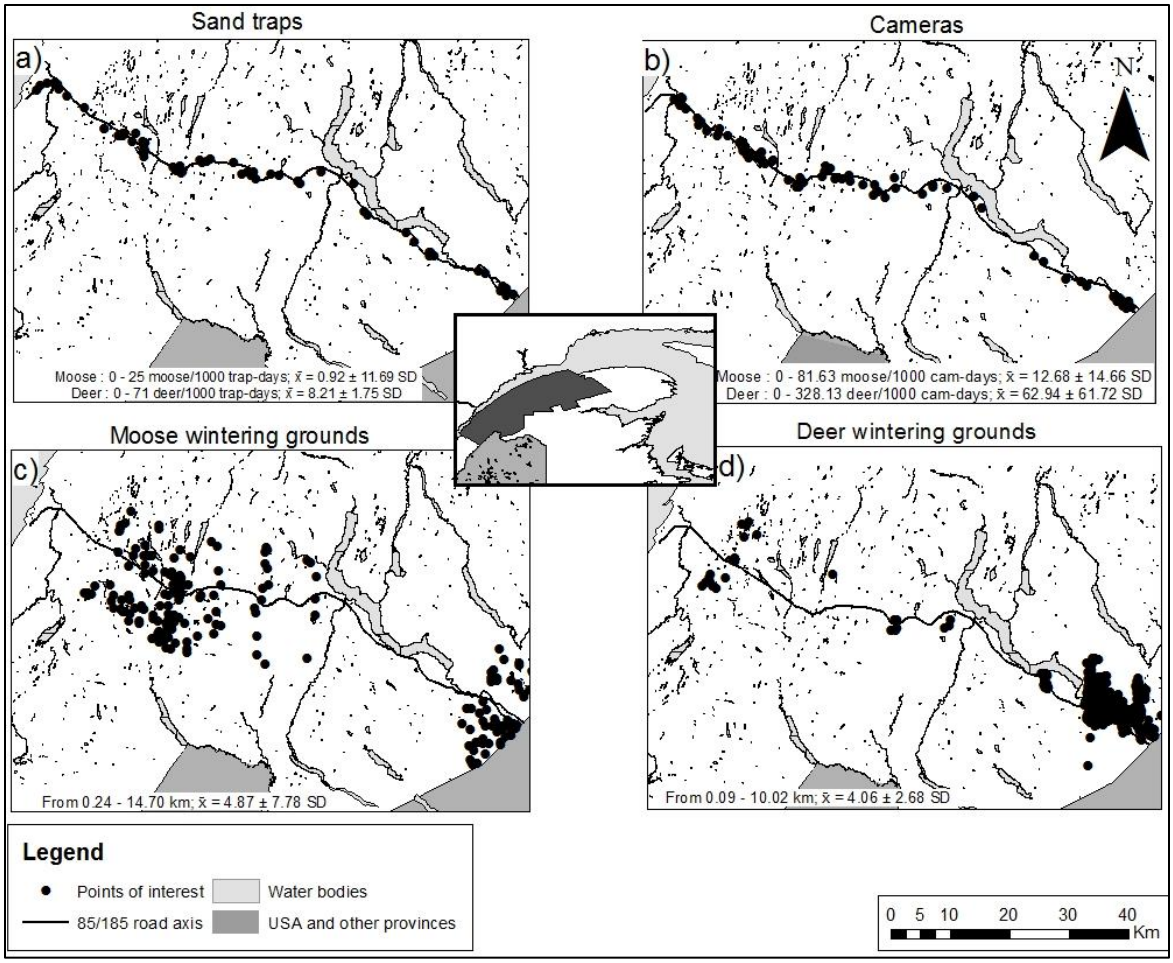

Figure 4. Location of sand traps (a), automated cameras (b), moose wintering grounds (c) and white-tailed deer wintering grounds (d) along the 85/185 road axis in southeastern Québec, Canada. Sand traps and cameras were deployed in the summer of 2017 while wintering grounds were surveyed by helicopter during the winter of 2016.

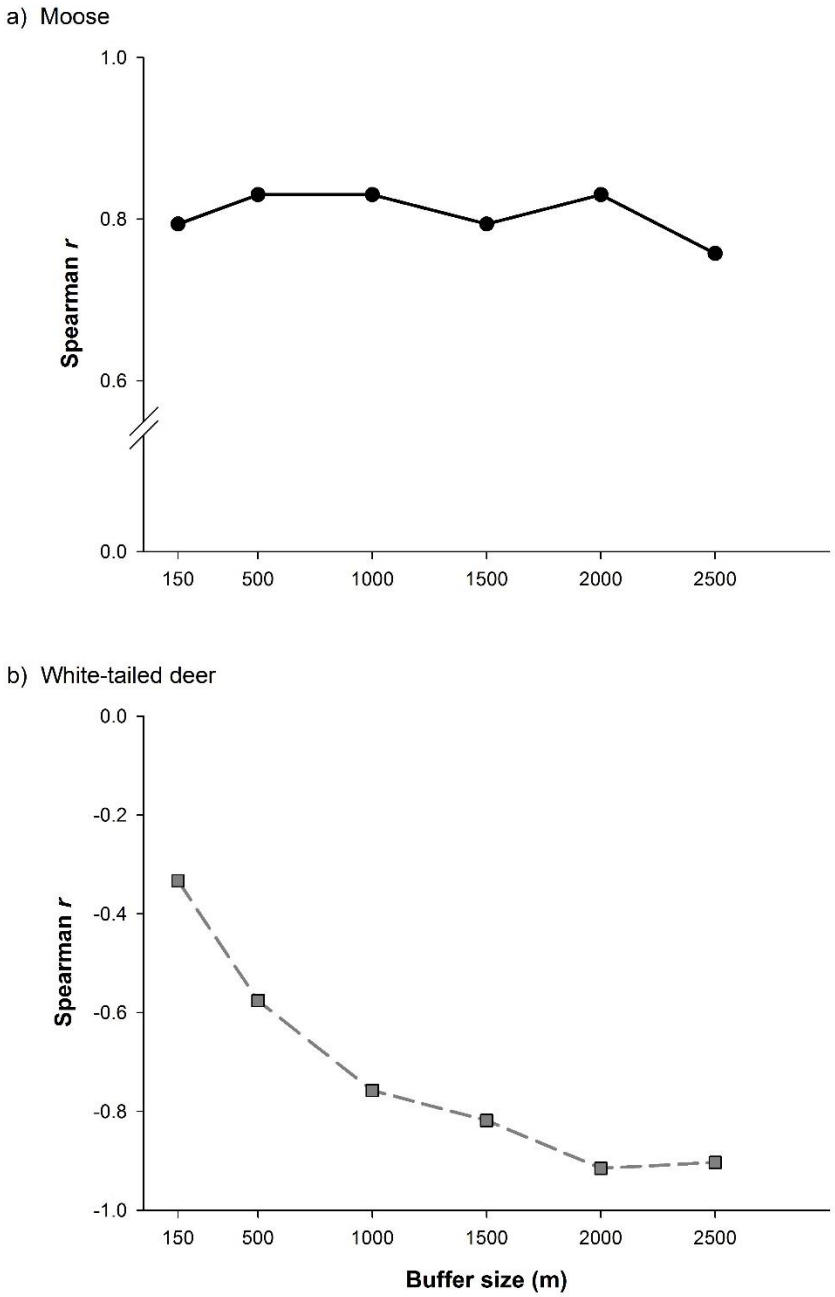

Figure 5. Effect of buffer size (as a proxy of spatial scale) on the correlation strength between moose connectivity modelled with *CircuitScape* and the detection rates by cameras (a) and on the correlation strength between deer connectivity modelled with *CircuitScape* and the dectection rates by sand traps (b) along the 85/185 road axis in southeastern Québec (Canada).

Table 1. Resistance values used to build the resistance rasters for functional connectivity modeling.

Components	Resistance value
1-RSF scores	1-100*
Wildlife crossing structures	80
Water bodies	300
Roads < 1000 AADT[1]	100
Roads 1000 – 4 999 AADT	200
Roads 5000 – 9 999 AADT	300
Roads ≥ 10,000 AADT	400
Buildings	500
Impermeable barriers	1000

* The inverse of RSF scores were multiplied by 100

[1] Annual Average Daily Traffic

Table 2. Correlation scores between both cervids' functionnal connectivity values obtained with *CircuitScape* and *LinkageMapper* and validation metrics (collision densities, distance to the nearest wintering grounds, detection rate by cameras and detection rate by sand traps

	Moose				White-tailed deer			
	CircuitScape		LinkageMapper		CircuitScape		LinkageMapper	
Collisions density (Adj. R^2)	$F_{(2,97)} = 6.39, p < 0.05$	0.10	$F_{(2,97)} = 30.72, p < 0.05$	0.38	$F_{(2,97)} = 19.44, p < 0.05$	0.27	$F_{(2,97)} = 9.69, p < 0.05$	0.15
Wintering grounds (Pearson's r)	$t_{(1,98)} = -4.20, p < 0.05$	-0.40	$t_{(1,98)} = 3.00, p < 0.05$	0.29	$t_{(1,98)} = 0.53, p = 0.6$	0.05	$t_{(1,98)} = 3.29, p < 0.05$	0.32
Cameras (Spearman's ρ)	$S = 28, p < 0.05$	0.83	$S = 144, p = 0.73$	0.12	$S = 82, p = 0.14$	0.51	$S = 126, p = 0.51$	0.26
Sand traps (Spearman's ρ)	$S = 68, p = 0.08$	0.59	$S = 224, p = 0.31$	-0.35	$S = 316, p < 0.05$	-0.92	$S = 76, p = 0.11$	0.54

SUPPLEMENTARY MATERIAL 1. MOOSE RESOURCE SELECTION FUNCTION (RSF)

We built the RSF for moose using data from 20 moose located in the Témiscouata region (southeastern Québec, Canada). Twenty adult moose (2 males and 18 females) were captured and collared (GPS/Iridium Vectronic Vertex Lite 3D, Keswick, Ontario, Canada) during winter 2017, but 5 were harvested by sport hunters in fall 2017. Captures and handling of study animals were approved by the Animal Welfare Committee (according to the guidelines of the Canadian Council on Animal Care) of the Université du Québec à Rimouski (certificates #CPA-68-17-183). An annual home range was delineated for each individual moose using a 95% Minimum Convex Polygon (MCP). GPS locations of each moose were then compared to the same number of random locations distributed within the home range boundaries using a mixed effects logistic regression.

Variables included in the RSF models were land-cover types, slope, elevation and distance to the nearest road and nearest water body. A decay distance transformation ($e^{-\alpha/d}$; Carpenter *et al.* 2010) with an alpha value of 50 was used to attenuate the influence of an increasing distance from roads and plateaud at a distance of 500 m. Variance Inflation Factor (VIF) and Condition Index were calculated to assess multicollinearity among variables. We pooled some habitat categories that had similar use/availability ratios in order to reduce the number of variables (k) in the model: water bodies were then grouped with wetlands, young clearcuts with old clearcuts and natural disturbances with regenerating stands. Mixed effects logistic regressions were used to identify the most parsimonious model and the collar ID was used as a random effect. Three candidate models were built to illustrate the different hypotheses related to habitat, topography or distance to the nearest road and interactions between those variables and the most parsimonious model was chosen using the BIC (Table S1).

This model contained land-cover types and distance to the nearest road (Table S1). Deciduous mature stands, water bodies, wetlands and "other" habitats were avoided by moose while immature stands and 0-20 year old clearcuts were selected (Table S2). Habitats far from roads were also selected. We assessed the robustness of this model using a k-fold

cross-validation (Boyce *et al.* 2002) in which the model was built using 75% of the dataset and validated against the remaining 25%, an operation repeated 49 times (i.e. 50 iterations). The most parsimonious model validation was robust (r_s = 90.63 ± 3.27 % (SD).

Table S2. Logistic regression candidate models built to explain relative occurrence probabilities of moose in the Rivière-du-Loup and Temiscouata regions, southeastern Quebec, Canada (n = 13). The most parsimonious model is shown in bold.

Model	k	n	ΔBIC
Habitat categories[1]	9	13	932
1 + Distance to the nearest road	**10**	**13**	**0**
2 + Squared distance to the nearest road	11	13	373

[1] Coniferous mature stands were used as the reference category in all RSF models.

Table S2. Coefficients (β) and 95% confidence interval of the most parsimonious model describing probability occurrence of moose in the Rivière-du-Loup and Temiscouata regions, southeastern Quebec, Canada. Coefficients for which the 95% CI did not overlap zero had a significant effect on the habitat selection patterns.

	β	[lower: upper 95% CI]
Intercept	-0.739	[-0.806: -0.672]
Deciduous mature stands	-0.282	[-0.329: -0.235]
Water bodies and wetlands	-1.252	[-1.405: -1.099]
Other	-0.456	[-0.542: -0.370]
Immature stands	0.341	[0.284: 0.398]
0-20 year old clearcuts	0.202	[0.158: 0.24512]
Natural disturbances and regenerating stands	0.024	[-0.027: 0.075]
Distance to nearest roads	0.94	[0.879: 1.001]

SUPPLEMENTARY MATERIAL 2. WHITE-TAILED DEER RESOURCE SELECTION FUNCTION

We calculated the resource selection function for white-tailed deer using data from Lesage *et al*. (2000) in which deer were captured and fitted with VHF collars. Deer were captured using Stephenson box traps in the Pohenegamook wintering area (PWA) from 1994 to 1997 and the Lake Temiscouata wintering range (LTWA) from 1994 to 1995 following standard techniques approved by the Animal Welfare Committee of the Université Laval. A total of 100 deer were captured throughout the study period; 38 immatures (16 males and 22 females) and 41 adult (18 males and 23 females) in the PWA and 12 immatures (4 males and 8 females) and 9 adults (2 males and 7 females) in the LTWA. Deer locations were estimated by triangulation with a GPS fixed station and the LOCATE II software (Pacer, Truro, N.S., Canada; Nams 1990). The real deer locations were compared to the same number of random locations in the entire study area based on habitat characteristics with a logistic regression.

Variables included in the models were habitat categories, slope, elevation and distance to the nearest road and nearest water body. The habitat categories were the same as mentioned earlier (see Methods section). Slope and elevation variables were contextualised in 500-m buffer zones around each locations.VIF and Condition Index were calculated to assess collinearity among variables. Logistic regressions were used to identify the most parsimonious model. Five candidate models were built based on different hypotheses related to habitat, topography or distance to the nearest road and interactions between those variables at the population level. The most parsimonious model was identified using the BIC (Table S3).

The most parsimonious model for deer contained habitat categories, slope, elevation, squared elevation, distance to the nearest road and nearest water body. This model suggest that water bodies and "other" habitats were avoided but old cuts, young cuts, natural disturbances and mature coniferous stands were selected, as were higher relative elevation and slope (Table S4). Habitats near water bodies and roads were also selected. The relation between the elevation and the squared elevation showed that deer selected habitats in intermediate elevations. We assessed the robustness of this model using a *k*-fold cross-

validation (Boyce *et al.* 2002) in which the model was tested on 25% of the complete dataset during 50 iterations. The cross-validation classified the outcome of the model with success in 95.22% (SD 2.77) of the cases.

Table S3. Logistic regression candidate models built to explain relative occurrence probabilities of white-tailed deer in the Rivière-du-Loup and Temiscouata regions, southeastern Quebec, Canada (n = 3 042). The most parsimonious model is shown in bold.

Model	k	n	ΔBIC
Habitat categories[1]	10	3042	205.33
1 + Topography	12	3042	113.41
1 + Distance to the nearest road + Distance to the nearest water body	12	3042	143.06
3 + Topography	14	3042	59.20
4 + Elevation + Elevation^2	**15**	**3042**	**0.00**

[1] Regenerating stands were used as the reference category in all RSF models.

Table S4. Coefficients (β) and 95% confidence interval of the most parsimonious model describing probability occurrence of white-tailed deer in the Riviere-du-Loup and Témiscouata regions situated in southeastern Québec (Canada) in 2017. Coefficients for which the 95% CI did not overlap zero had a significant effect on the habitat selection patterns.

	β	[lower: upper 95% CI]
Intercept	-1.117	[-1.570: -0.664]
Mature deciduous stands	0.195	[-0.045: 0.436]
Water	-2.419	[-3.141: -1.697]
Other	-0.708	[-0.959: -0.458]
Immature stands	-0.017	[-0.239: 0.205]
Old cuts	0.830	[0.575: 1.084]
Young cuts	0.677	[0.362: 0.992]
Natural disturbances	0.792	[0.468: 1.116]
Wetlands	-0.457	[-1.002: 0.089]
Mature coniferous stands	0.359	[0.074: 0.643]
Human	-0.310	[-0.842: 0.222]
Distance to nearest road	-0.554	[-0.868: -0.24]
Distance to nearest water body	-0.292	[-0.377: -0.207]
Elevation	9.406	[6.645: 12.168]
Elevation^2	-19.249	[-23.964: -14.534]
Slope	0.116	[0.092: 0.14]

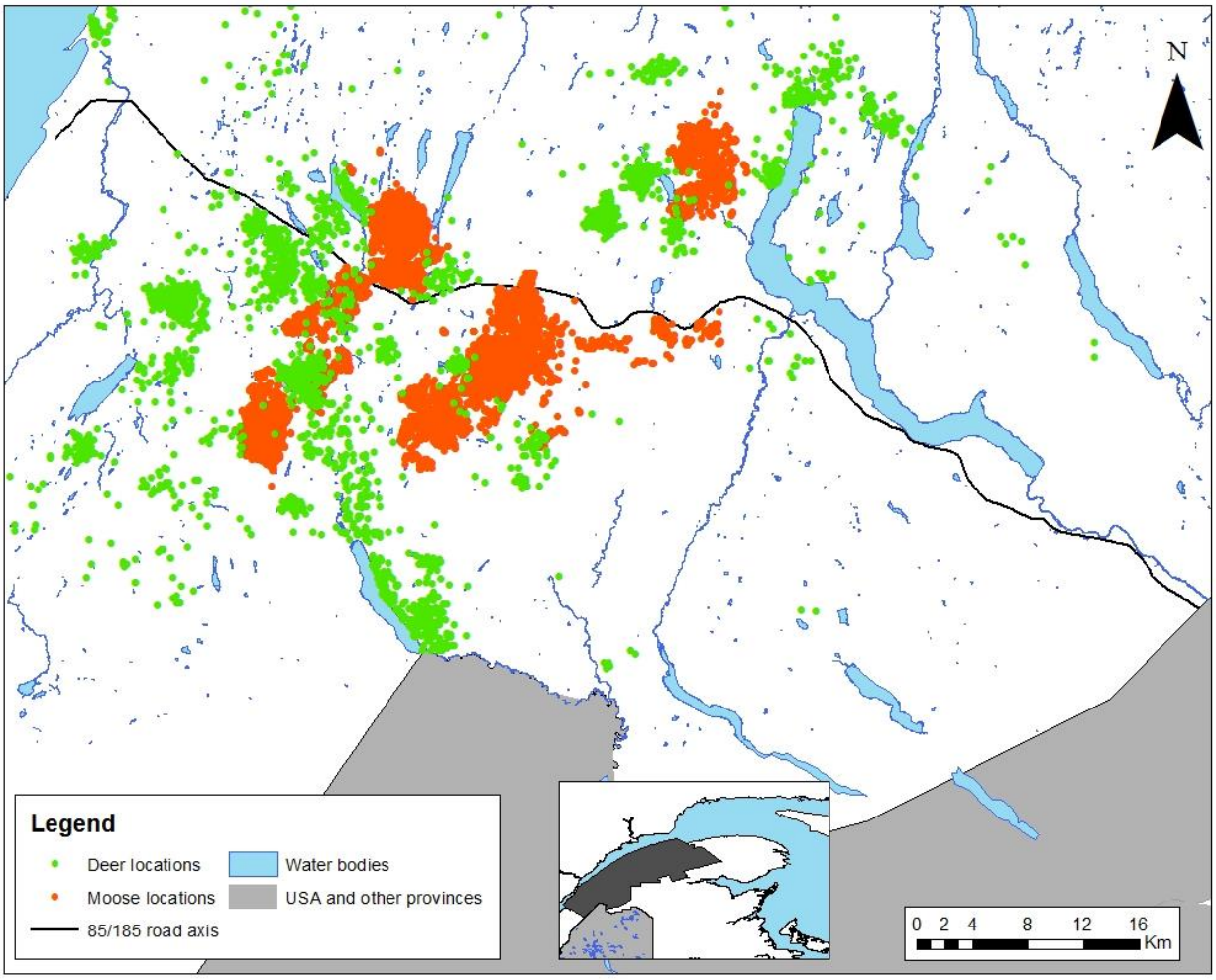

Figure S1. Locations of radiocollared moose (orange) and white-tailed deer (green) in the Rivière-du-Loup and Témiscouata regions in southeastern Québec, Canada.

CONCLUSION GÉNÉRALE

En Amérique du Nord, les stratégies d'atténuation des collisions routières avec la faune ont longtemps été davantage réactives que préventives jusqu'à présent, puisque les mesures sont souvent mises en place suite à l'identification d'une zone problématique où se concentre un nombre important de collisions routières (Clevenger *et al.* 2006 ; Shiling & Waetjen 2015). De plus, lorsque des structures d'atténuation (p. ex. clôtures d'exclusion de la grande faune, passages fauniques sous la chaussée) sont prévues dans les développements routiers, leur emplacement est souvent sélectionné pour des raisons logistiques et/ou hydrologiques (p. ex. possibilité d'élargir un ponceau) plutôt qu'en raison d'une utilisation démontrée par la faune (van der Grift 2005). Or, l'adoption d'une stratégie proactive d'atténuation des collisions routières impliquant la faune pourrait permettre d'intégrer ces structures dès le départ aux plans de conception et aux phases préliminaires de construction lors de projets routiers et ainsi éviter les coûts de construction *a posteriori*, diminuer les risques de collisions avec la faune et permettre de conserver une bonne connectivité fonctionnelle de part et d'autre de la route. Cependant, considérant les coûts élevés et les préoccupations tant éthiques que biologiques (c.-à-d. maintien de la connectivité) reliées au fait de clôturer l'entièreté des routes, des animaux sont susceptibles de se retrouver sur la chaussée dans les secteurs non clôturés et d'ainsi représenter un risque pour les usagers de la route. Il est donc important de sensibiliser ces usagers aux risques de collision avec la faune dans les secteurs plus favorables aux traversées par la faune. Considérant la menace pour la sécurité routière (Bissonette *et al*. 2008) et l'importance économique que représente les collisions routières avec la faune (Huijser *et al.* 2008, 2009), il s'avère essentiel de développer des outils nous permettant de fournir les connaissances nécessaires aux gestionnaires et aux décideurs afin d'intégrer des considérations fauniques dès le début des projets d'infrastructures routières.

OBJECTIFS

L'objectif principal de cette étude était donc de développer une méthodologie permettant de modéliser et de valider la présence de corridors fauniques dans le cadre de projets routiers. Cet objectif se divisait en deux sous-objectifs complémentaires. Tout d'abord, nous souhaitions identifier les zones à risque (c.-à-d. une zone où les risques de collisions sont plus élevés que sur la majorité de l'axe routier) en caractérisant la distribution spatiotemporelle des collisions impliquant les cervidés sur l'axe routier 85/185. La deuxième étape sous-jacente à l'élaboration d'une bonne stratégie d'atténuation des collisions avec la faune consiste à modéliser la connectivité fonctionnelle de part et d'autre de la route. Par conséquent, notre deuxième sous-objectif était d'identifier et valider les corridors de déplacements de la faune afin de déterminer les zones prioritaires pour l'aménagement de structures d'atténuation des collisions.

RETOUR SUR LES PRINCIPAUX RÉSULTATS

COLLISIONS ROUTIÈRES IMPLIQUANT LES CERVIDÉS

Les résultats que nous avons obtenus dans l'analyse des caractéristiques spatiotemporelles aux sites de collisions impliquant l'orignal et le cerf de Virginie ont permis de montrer que les aspects temporel et spatial jouaient un rôle important dans la distribution des collisions mais à des niveaux différents selon l'espèce impliquée (Chapitre 1). Un partitionnement de la variance nous a permis de montrer que les caractéristiques temporelles expliquaient une grande partie de la variation des collisions avec les deux espèces de cervidés, tant entre les mois de l'année qu'entre les phases du jour. Une augmentation du nombre de collisions à l'approche du printemps et un maximum au milieu de l'été était visible pour les collisions avec l'orignal alors que la distribution mensuelle des collisions impliquant le cerf démontrait un premier maximum en avril suivi d'une deuxième augmentation du nombre de collisions à l'automne, culminant avec un maximum en septembre. Ces deux distributions concordent avec des périodes biologiques importantes pour les cervidés où les taux de déplacements sont plus élevés (p.ex. dispersion post-natale; Long *et al.* 2005; Putzu

et al. 2015 et reproduction; Stickles *et al.* 2016; Whitman *et al.* 2018) et où les cervidés utilisaient davantage les habitats à proximité des routes (Leblond *et al.* 2007). Les distributions temporelles des collisions étaient relativement similaires pour les deux espèces en ce qui concernait les phases du jour, avec un nombre de collisions plus important à l'aube et au crépuscule, sans différence entre ces deux phases, ce qui correspond aux périodes journalières où les cervidés sont les plus actifs (Ager *et al.* 2003). Le nombre de collisions était également plus élevé durant la nuit que durant le jour. Cependant, il se produisait plus de collisions impliquant l'orignal que le cerf de Virginie durant la nuit. Pour ce qui est des caractéristiques spatiales, nos résultats suggèrent que le risque de collision avec un orignal était principalement influencé par les variables topographiques. En effet, le risque de collision était influencé par l'altitude et la pente en plus de la distance à une parcelle de bon habitat. De plus, des interactions entre la pente et l'altitude et entre la pente et la distance à une parcelle de bon habitat ont mis en évidence l'augmentation du risque de collision lorsque la pente est faible, témoignant de la tendance qu'ont les orignaux à se déplacer en suivant les courbes de niveau (Leblond *et al.* 2010). L'effet de la pente et de l'altitude peut également être lié à la capacité des conducteurs à détecter un animal présent sur la route, influençant ainsi le temps de réaction, une variable qui influence souvent la probabilité de collision (Rea *et al.* 2018). Ces interactions ont également permis de montrer que le risque de collision peut également être élevé lorsque l'on se retrouve loin des parcelles de bon habitat. Ce dernier résultat va à l'encontre de plusieurs études qui ont mis en évidence la relation négative entre la distance aux parcelles de bons habitats et le risque de collision (Rolandsen *et al.* 2011; Hothorn *et al.* 2015). Nous avons donc été en mesure de montrer que cette relation n'est pas toujours linéaire et peut interagir avec d'autres variables (p. ex. la pente).

La robustesse du modèle expliquant la distribution spatiale des collisions impliquant le cerf de Virginie était relativement faible. Ceci nous porte à croire que la variabilité dans la distribution des collisions avec ce cervidé est moinsexpliquée par les variables que nous avons considérées, les collisions semblant par conséquent plutôt aléatoirement distribuées dans l'espace et/ou davantage expliquées par les variables temporelles. Bien que certaines autres études ont été en mesure de relier la distribution des collisions routières impliquant la

faune avec le débit routier (Rowden *et al.* 2008; Morelle *et al.* 2013; Kazemi *et al.* 2016), les résultats de nos analyses concordent avec ceux d'autres études (Dussault *et al.* 2006; Hothorn *et al.* 2015; Krauze-Grytz *et al.* 2017) en mettant en évidence que les patrons de déplacements des cervidés sont le principal facteur influençant la distribution spatiale des collisions avec ceux-ci. Nous avons toutefois franchi un pas supplémentaire comparativement à ces dernières études en montrant que certaines variables peuvent interagir entre elles et mieux expliquer la distribution des collisions que seulement leur effet simple.

CONNECTIVITÉ FONCTIONNELLE

Dans le deuxième chapitre, nous avons évalué le pouvoir de validation de certaines variables (densités de collisions routières, distance au ravage le plus près, taux de détection par les caméras et taux de détection par les trappes à sable) afin d'identifier celles appropriées pour valider ce type de modèle. Nous avons mis en évidence la grande variabilité d'efficacité entre les approches utilisées pour valider ce type de modèle. En effet, l'intensité de la corrélation lors des validations variait entre les espèces étudiées, les méthodes employées pour modéliser la connectivité (c.-à-d. *CircuitScape* et *LinkageMapper*), les métriques utilisées pour valider les modèles ainsi qu'entre les échelles spatiales considérées. Les corridors de déplacement modélisés pour l'orignal se concentraient principalement au centre de notre aire d'étude alors que ceux pour le cerf de Virginie se retrouvaient surtout au nord de l'axe routier. Les corridors de connectivité modélisés avec *CircuitScape* étaient plus circonvolués alors que ceux modélisés avec *LinkageMapper* étaient plutôt rectilignes, ce qui pourrait être dû au fait que la matrice de résistance était plutôt hétérogène dans notre aire d'étude (Rayfield *et al.* 2010; Koenig et Bender 2018). Nos analyses ont également montré que la densité de collisions routières et la distance au ravage n'étaient pas ou peu appropriées pour valider des modèles de connectivité fonctionnelle dans notre système d'étude. Ceci s'expliquait par le fait que la densité de collisions routières ne capture qu'une partie des mouvements des animaux, à savoir ceux où des animauxentrent en collision avec une voiture. Les animaux qui réussissent à traverser la route ne sont donc jamais comptabilisés. Pour ce

qui est de la distance au ravage, cette variable pourrait être appropriée que durant une courte période de l'année (c.-à-d. les migrations pré- et post-hivernales ainsi que l'hiver) puisque les cervidés utilisent des habitats différents durant l'été et l'hiver (Porter *et al.* 2004; Hurst & Porter 2008) et peuvent effectuer de longs déplacements entre ceux-ci (Dussault *et al.* 2005). Par contre, le taux de détection par les caméras était mieux corrélé à la connectivité modélisée, traduisant la fiabilité et l'efficacité de cette méthode d'inventaire pour étudier la distribution et les mouvements de la faune (Tobler *et al.* 2008; Lyra-Jorge *et al.* 2008; Rowcliffe *et al.* 2011). Ceci n'était pas le cas pour le taux de détection par les trappes à sable alors que la corrélation avec les valeurs de connectivité étaient négatives, suggérant une quasi-absence de relation. En comparaison aux caméras automatiques, l'utilisation des trappes à sable présente deux problèmes majeurs, à savoir que 1) l'identification des espèces est plus difficile et que 2) les trappes à sable sont plus sujettes aux intempéries (p. ex. pluie, sécheresse, pistes superposées) (Ford *et al.* 2009). De plus, nos résultats ont montré que l'intensité de la validation variait selon l'échelle spatiale à laquelle la connectivité était considérée. En effet, la variabilité associée à l'échelle spatiale différait selon l'espèce étudiée, probablement en lien avec leur capacité de dispersion respective (Wheatley & Johnson 2009; Vogt *et al.* 2009; Lechner *et al.* 2017). Cet effet de l'échelle spatiale pourrait aussi être lié à l'échelle temporelle, puisque les déplacements quotidiens sont probablement davantage perceptibles à fine échelle spatiale alors que les grands déplacements (p. ex. migrations) le seraient davantage à large échelle spatiale. Dans ce chapitre, nous avons poussé la réflexion un peu plus loin que plusieurs études traitant de connectivité fonctionnelle (p. ex. Walpole *et al.* 2012; Koen *et al.* 2014; Marrotte *et al.* 2017) en validant empiriquement nos modèles théoriques de connectivité. De plus, contrairement à des études qui avaient elles aussi validé leurs modèles (p. ex. Riggio et Caro 2017; Vanthomme *et al.* 2018), nous avons utilisé plusieurs métriques différentes pour valider nos modèles, permettant du coup une comparaison entre les approches utilisées. Nous avons donc été en mesure d'identifier le modèle le plus approprié pour cartographier la connectivité fonctionnelle dans notre aire d'étude, mais également l'approche la plus appropriée pour valider ce modèle. Dans notre

cas, l'utilisation de données de déplacement réels d'animaux appliquées à l'échelle adéquate nous a permis de bien contextualiser ces déplacements.

CONTRIBUTIONS APPLIQUÉES À L'ÉCOLOGIE ROUTIÈRE

Du point de vue appliqué, nos résultats contribuent à améliorer la stratégie d'atténuation des collisions routières impliquant la faune sur l'axe routier 85/185, un tronçon actuellement en construction afin de le faire passer d'une route provinciale à 2 voies à une autoroute provinciale à 4 voies séparées par un terre-plein. Dans ce cas particulier, nos résultats ont permis de cartographier le risque d'entrer en collision avec l'une ou l'autre des deux espèces

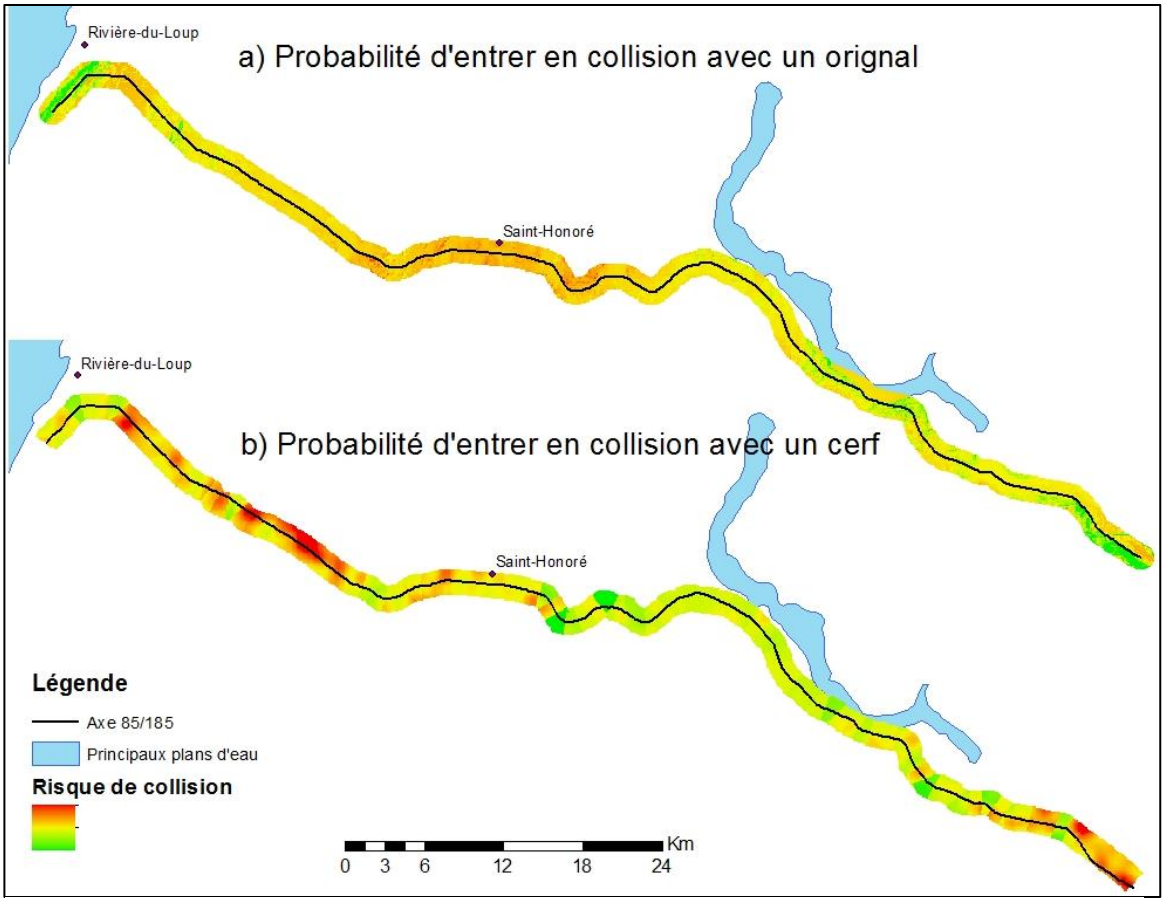

Figure 1. Modélisation du risque de collision impliquant l'orignal (a) et le cerf de Virginie (b) sur l'axe routier 85/185 dans la région du Témiscouata, Québec, Canada.

ciblées par notre étude (orignal : Figure 1a ; cerf de Virginie : Figure 1b ci-dessous ; voir aussi Chapitre 1). Connaître les zones et les périodes les plus à risque pour les collisions impliquant ces deux espèces de grands ongulés permet par conséquent aux autorités du Ministère des Transports, de la Mobilité durable et de l'Électrification des transports (MTMDET) d'ajuster les mesures d'atténuation de manière adéquate. Parmi les retombées potentielles de nos travaux, notons la possibilité de limiter l'accès des cervidés à la route et de sensibiliser les usagers aux risques que ces animaux représentent afin d'ultimement influencer le comportement des conducteurs. Nos résultats permettent donc de concentrer les efforts d'atténuation sur la principale facette qui semble moduler la distribution et la fréquence des collisions, à savoir les patrons de déplacements des cervidés.

De plus, l'analyse de connectivité fonctionnelle réalisée au chapitre 2 permet d'identifier les tronçons routiers où la probabilité de traversée (et non juste le risque de collision, comme dans le chapitre 1) est importante, des tronçons qui peuvent potentiellement représenter des risques pour la sécurité des usagers (Figure 2a). L'identification des corridors de connectivité pour les deux espèces cibles permettra aux autorités du MTMDET de mettre en place une stratégie d'atténuation des collisions routières impliquant la faune qui contribuera à l'amélioration de la sécurité routière tout en maintenant une bonne connectivité pour la faune entre les habitats de qualité situés de part et d'autre de la route. Il est également possible d'appliquer nos modèles de connectivité fonctionnelle à des différents scénarios qui combinent différentes structures d'atténuation de manière à illustrer et quantifier l'effet des mesures sur la connectivité fonctionnelle et ultimement orienter la prise de décision en faveur d'une amélioration de la sécurité routière (Figure 2b). À l'aide de cette approche, il est possible de positionner les traversées fauniques vers les endroits les plus appropriés, faisant en sorte de limiter les incursions sur la route.

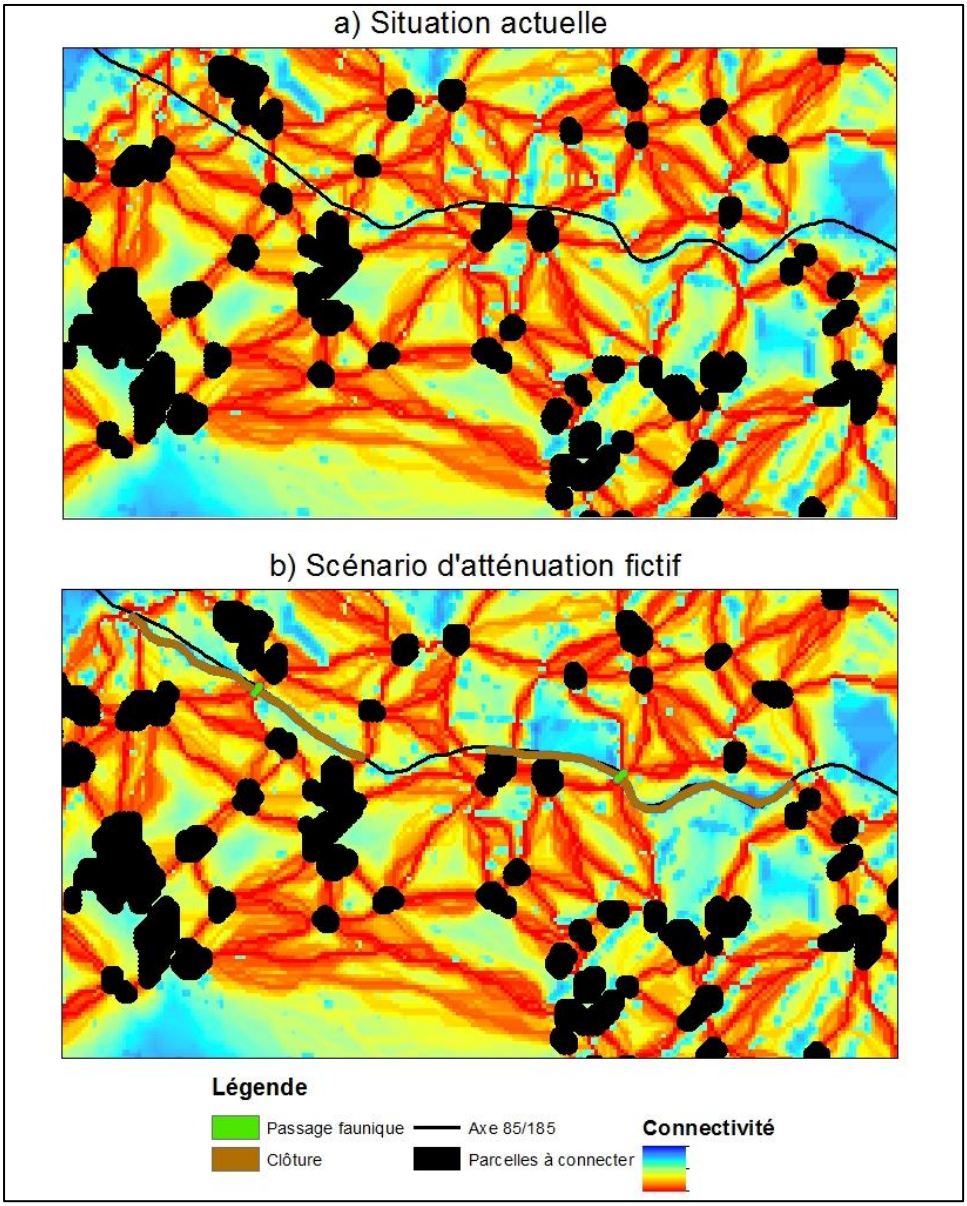

Figure 2. Scénarios actuel (a) et fictif (b) de l'impact de l'installation de différentes structures d'atténuation des risques de collisions routières impliquant la faune sur la connectivité fonctionnelle sur un tronçon de l'axe routier 85/185 dans la région du Témiscouata, Québec, Canada.

CONTRIBUTIONS THÉORIQUES

Les résultats du premier chapitre mettent en évidence que les patrons de déplacements des cervidés ainsi que leur comportement expliquent une bonne part de la variation dans la distribution spatiotemporelle des collisions routières. Nos résultats montrent l'importance d'étudier la distribution temporelle des collisions en plus de la distribution spatiale car l'aspect spatial pourrait n'expliquer qu'une faible part de la variabilité (p. ex. pour le cerf de Virginie dans notre cas). Toutefois, l'un des points les plus intéressants provenant de nos résultats est l'interaction entre la pente et l'altitude ainsi qu'entre la pente et la distance à une parcelle d'habitat de bonne qualité dans nos analyses de distribution spatiale des collisions avec l'orignal. En effet, il est très intéressant de voir que la relation entre l'altitude et le risque de collision ainsi que la distance à une parcelle d'habitat de bonne qualité diffèrent selon la pente. De plus, plusieurs études ont tenté d'expliquer la distribution des collisions routières impliquant la faune avec des métriques du paysage (Tanner *et al.* 2017; Jakubas *et al.* 2018; Canal *et al.* 2018; Hegland et Hamre 2018) mais à notre connaissance, aucune n'a intégré des interactions entre les variables afin d'expliquer cette distribution. Ceci suggère que certaines valeurs peuvent interagir entre elles et avoir une relation non linéaire avec le risque de collision, ce qui constitue un ajout important dans l'explication de la distribution spatiale des collisions impliquant la faune.

Dans le deuxième chapitre, nous avons mis en évidence que la validation des modèles de connectivité avec des données empiriques est une étape cruciale qui ne devrait pas être négligée et qui devrait faire partie intégrante d'une analyse de connectivité fonctionnelle fiable et robuste. De plus, ce chapitre a permis de souligner que certaines métriques reflètent mieux les variations spatiales de connectivité fonctionnelle que d'autres, soulignant ainsi l'importance de bien sélectionner ces métriques en amont d'un exercice de validation. Dans le cas présent, le processus de validation a également permis de montrer que certains modèles de connectivité ne représentent pas la réalité avec certitude, mettant encore plus l'accent sur l'importance de valider ces derniers modèles. En effet, nous avons démontré que l'utilisation de *CircuitScape* était plus appropriée dans une aire d'étude où la matrice du paysage n'offrait

pas beaucoup de résistance aux déplacements des individus (Rayfield *et al.* 2010; Koenig et Bender 2018). Tout comme pour la modélisation de la sélection d'habitat, nos résultats témoignent de l'importance de bien choisir l'échelle spatiale à laquelle les analyses de connectivité fonctionnelle sont réalisées puisque la robustesse de la validation de ces modèles semblait varier entre les échelles considérées en plus de différer selon l'espèce ciblée.

LIMITES DE L'ÉTUDE

Certaines limitations s'appliquent aux modèles de connectivité utilisés dans la présente étude. Tout d'abord, l'emplacement des corridors modélisés pourrait être – en partie du moins – le résultat d'un artefact de modélisation puisque les limites de l'aire d'étude pourraient être perçues comme des barrières artificielles par le modèle, suggérant qu'au-delà de ces limites, il n'y a plus d'habitat disponible (Koen *et al.* 2010; 2012; Gangadharan *et al.* 2017). Afin d'éviter ce problème, Koen *et al.* (2010) ont suggéré d'utiliser une zone tampon autour de l'aire d'étude et d'y placer les parcelles d'habitat à connecter. De plus, les résultats d'analyses de connectivité dépendent grandement du type de données utilisées pour construire les matrices de résistance (Zeller *et al.* 2018). En effet, plusieurs types de données (p. ex. opinions d'experts, sondages, inventaires de pistes, localisations GPS) peuvent être utilisées pour évaluer la qualité d'habitat pour une espèce donnée, toutes ces méthodes ont leur propre précision et exactitude (Rettie & McLoughlin 1999; Tyre *et al.* 2003; Frair *et al.* 2004; Johnson & Gillingham 2004) et les résultats de connectivité qui en découlent peuvent différer. La transformation utilisée pour convertir la qualité de l'habitat en valeurs de résistance pourrait également être un facteur additionnel pouvant influencer les résultats d'analyses de connectivité (Keeley *et al.* 2016; 2017; Zeller *et al.* 2018). Les méthodes les plus souvent employées sont les fonctions linéaires négatives (Chetkiewicz & Boyce 2009) et les fonctions exponentielles négatives (Keeley *et al.* 2017). Il serait donc recommandé de tester ces différentes méthodes afin d'identifier la transformation la plus appropriée pour l'aire à l'étude (Keeley *et al.* 2016). Finalement, la puissance de calcul est souvent une des plus importantes limites à la modélisation de la connectivité et ce, peu importe l'approche

préconisée (p. ex. modèles de circuits ou de trajets de moindre coût), étant contrainte par l'échelle spatiale considérée (c.-à-d. la taille de la zone) et la résolution spatiale souhaitée (Moilanen 2011; Leonard *et al.* 2016).

CONCLUSIONS ET PERSPECTIVES

Dans un contexte où le réseau routier est continuellement en expansion (Hawbaker *et al.* 2006), il est important de se doter d'une méthode proactive d'identification des zones prioritaires pour l'aménagement de structures d'atténuation dans le cadre de projets routiers (Simberloff *et al.* 1992). Ce mémoire souligne l'importance d'intégrer la planification de l'aménagement de structures d'atténuation des collisions impliquant la faune (p. ex. clôtures et passages sous la chaussée) dès le début des projets routiers, au bénéfice d'une gestion intégrée des risques pour les usagers de la route.

Il serait intéressant d'analyser la stabilité des facteurs influençant le risque de collision afin d'évaluer si ceux-ci varient temporellement (Behnood & Mannering 2015). Il serait pertinent de mettre en place un suivi à long terme de l'utilisation des structures d'atténuation par la faune afin de documenter et caractériser l'efficacité de celles-ci (McCollister et van Manen 2010). Ceci permettrait de pouvoir identifier quel type d'ouvrage est le plus efficace dans le but de concentrer les efforts de construction sur les structures les plus appropriées et ainsi permettre une meilleure perméabilité de la route, le tout en assurant la sécurité routière pour les usagers de la route. Tel que souligné par van der Grift *et al.* (2013), l'utilisation d'un passage ne représente pas nécessairement son efficacité et les protocoles de suivis sont souvent mal conçus car souvent trop courts ou parce qu'ils ne prennent pas en compte les phases pré-construction. Conséquemment, les protocoles scientifiques doivent être impliqués le plus tôt possible dans le développement de chantiers routiers (Rytwinski *et al.* 2015) afin de permettre de mieux prévenir les collisions impliquant la faune et des véhicules (Santos *et al.* 2018). Ceci est particulièrement vrai si l'on considère que les structures d'atténuation varient grandement en efficacité et en coût de construction (Rytwinski *et al.* 2016). De plus,

des analyses spatiales supplémentaires pourraient être effectuées en divisant la base de données de collisions en saisons (ou périodes biologiques) de manière à évaluer si les facteurs influençant la distribution des collisions avec la faune changent en fonction de fenêtres temporelles considérées.

Il serait également justifié d'effectuer certaines validations supplémentaires de la connectivité fonctionnelle. En effet, il serait possible de comparer les modèles de connectivité issus des modèles théoriques avec des données de déplacements réels issues d'animaux porteurs de colliers émetteurs, tel que décrit par Naidoo *et al.* (2018) chez l'éléphant d'Afrique. Ceci permettrait ainsi de faire une double validation des modèles et de s'assurer que la connectivité modélisée reflète effectivement les déplacements de la faune de la région. Il serait également possible de comparer les modèles de connectivité avec un modèle nul où la résistance du paysage serait fixée à 0 pour l'entièreté de la zone d'étude afin de déterminer s'il y a une différence entre le chemin le plus court entre les parcelles et les corridors modélisés, tel que décrit par McClure *et al.* (2016) et appliqué par Bond *et al.* (2017). Selon Keeley *et al.* (2018), la clé pour une stratégie efficace de maintien de la connectivité est de développer une vision commune entre tous les acteurs liés au projet (p.ex. chercheurs, promoteurs, usagers) et d'utiliser des données empiriques pour prioriser et valider les corridors de connectivité.

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